THE SKULL OF THE HERBIVOROUS SYNAPSID *EDAPHOSAURUS BOANERGES* FROM THE LOWER PERMIAN OF TEXAS

by S. P. MODESTO

ABSTRACT. The cranial anatomy of the Lower Permian synapsid *Edaphosaurus boanerges* is described, based upon well-preserved material from the Geraldine Bonebed (Wichita Group: Nocona Formation) of north-central Texas. Two autapomorphies for this species are identified: (1) 120–150 teeth are present on each palatal tooth plate; and (2) the mandibular symphysis is deeply excavated dorsally. Phylogenetic analysis of the interrelationships of *Edaphosaurus* species supports the hypotheses that the Lower Permian Texan species *E. boanerges*, *E. cruciger*, and *E. pogonias* are a monophyletic group, and *E. boanerges* is excluded from a clade formed by *E. cruciger* and *E. pogonias*. The suite of cranial specializations that characterizes *Edaphosaurus* is interpreted as an adaptation complex towards terrestrial herbivory. Isodonty, the presence of cutting edges on the marginal teeth, the oblique orientation of the cutting edges, and the shouldering of the marginal teeth, indicate that the anterior marginal teeth of *E. boanerges* served to crop bite-sized portions from tough, terrestrial plants. The food was then triturated by the palatal and mandibular tooth plates; minor grinding was provided also by the procumbent posterior teeth of the maxilla and dentary. The morphology of the jaw suspension indicates that the mandible was capable of fore-and-aft translation; the orientation of tooth plate occlusal surfaces and palatal tooth wear in *E. boanerges* indicate that propalinal movement was a major component of the grinding phase during oral food processing. The dual organization of the feeding system in *Edaphosaurus* is the earliest known example of its kind among amniotes.

THE Permo-Carboniferous is arguably one of the most interesting times in amniote evolutionary history, for it was during this time that the first large terrestrial herbivorous and carnivorous vertebrates appeared. The edaphosaurid synapsid genus *Edaphosaurus* was one of the most abundant, widespread and long-lived of the large herbivores.

Edaphosaurus is currently recognized as the oldest known genus of herbivorous amniote (Modesto and Reisz 1992). Recent studies have identified two small faunivorous taxa, *Ianthasaurus* and *Glaucosaurus* (Reisz and Berman 1986; Modesto 1994), as basal edaphosaurids. Accordingly, the presence of both faunivorous and herbivorous taxa within Edaphosauridae makes the family an indispensable component of investigations into the origins of terrestrial vertebrate herbivory (Modesto 1992).

Although *Edaphosaurus* has been known for well over one hundred years, its presence at many edaphosaurid localities is indicated only by fragments of the distinctive neural spines. Most species assigned to *Edaphosaurus* are represented by one or two poorly preserved skeletons, and the occasional tooth plate or isolated appendicular elements. Accordingly, our knowledge of the cranial anatomy of *Edaphosaurus* is imperfect. Most of what is known is based mainly upon descriptions of a single flattened and incomplete skull, the holotype of *Edaphosaurus pogonias* (Case 1906; Broom 1910; Watson 1916; Romer and Price 1940). Romer and Price (1940) were the last workers to describe this specimen. Although their description of the skull is now known to feature several major errors (Brinkman and Eberth 1983), recent studies (e.g. Olson 1986; Reisz 1986; Carroll 1988) continued to refer to it.

Interestingly, exceptionally preserved cranial materials attributed to *E. boanerges* have been available since the publication of Romer and Price's (1940) *Review of the Pelycosauria*. Between

1934 and 1941, an unprecedented amount of edaphosaurid material was recovered from the Geraldine Bonebed in Archer County, Texas (Wichita Group: Nocona Formation) by Harvard and Amherst College field parties. The remains of at least fourteen skeletons of this species were collected, including several complete, articulated skulls (Sander 1987). Accordingly, the material from Geraldine has made *E. boanerges* the best known member of the genus. However, that label does not extend to the cranial morphology, since the original description of *E. boanerges* (Romer and Price 1940) was based upon materials collected by Romer during the 1934 excavation, which apparently produced complete jaws but only a few disarticulated cranial elements. Romer and Price's (1940) reconstruction of the skull of *E. boanerges* appears to be a reworking of their reconstruction of the skull of *E. pogonias*, since most of the sutures are represented by dashed lines. The skulls collected during the 1939 and 1941 excavations were partially prepared, but only to serve as the basis for exhibition models. More recently, these specimens were used in a review of early synapsid phylogeny (Brinkman and Eberth 1983).

The rich assemblage of Geraldine materials provides an opportunity to describe thoroughly the cranial osteology of an edaphosaurid. The exceptional preservation of the tooth-bearing elements of the Geraldine skulls also permits an investigation into the adaptation to herbivory that has long been attributed to *Edaphosaurus*. This hypothesis was prompted by the presence of the large denticulate plates on the palate and the lingual surface of the mandible, and the presence of a large, barrel-shaped body. Most edaphosaurid marginal dentitions that were available to early workers were not well preserved, and accordingly did not figure in their hypotheses concerning diet. The well preserved Geraldine materials shed additional light on edaphosaurid herbivory.

This description and restudy of the skull of *Edaphosaurus boanerges* is essential in the light of recent systematic studies of early amniotes, for much remains to be clarified concerning the relationships of primitive synapsids. The goals of this work are to provide a detailed description of the skull of *Edaphosaurus boanerges*, to determine its probable feeding mechanism, to strengthen the hypothesis of herbivory attributed to this genus using the new cranial data, and to provide a robust phylogeny for *Edaphosaurus*.

Institutional abbreviations. AMNH, American Museum of Natural History, New York; MCZ, Museum of Comparative Zoology, Harvard University; ROM, Royal Ontario Museum, Toronto.

SYSTEMATIC PALAEONTOLOGY

SYNAPSIDA Osborn, 1903
EUPELYCOSAURIA Kemp, 1982
Family EDAPHOSAURIDAE Cope, 1882

Genus EDAPHOSAURUS Cope, 1882

Type species. Edaphosaurus pogonias Cope, 1882

Diagnosis. Edaphosaurids (see Modesto and Reisz 1990 for familial diagnosis) with small skulls, approximately equal in length to five dorsal centra; posterior process of the postorbital short, does not extend posterior to the level of the parietal foramen; nasal is approximately three-quarters the length of the frontal; frontal anterior process reduced in antero-posterior length to one-third frontal sagittal length; posterior cheek deeply emarginated; tooth plates are developed on the palate and the inner aspect of the mandible; palatal tooth plates are formed by the palatine, ectopterygoid, and pterygoid; mandibular tooth plates are formed by anterior coronoid, posterior coronoid, and prearticular; marginal teeth are isodont, slightly swollen distally, and feature fine serrated tips that curve slightly backwards; cutting edges of the cheek teeth are inclined obliquely with respect to the axis of the tooth row. Maxillary teeth become increasingly laterally directed posteriorly, while the
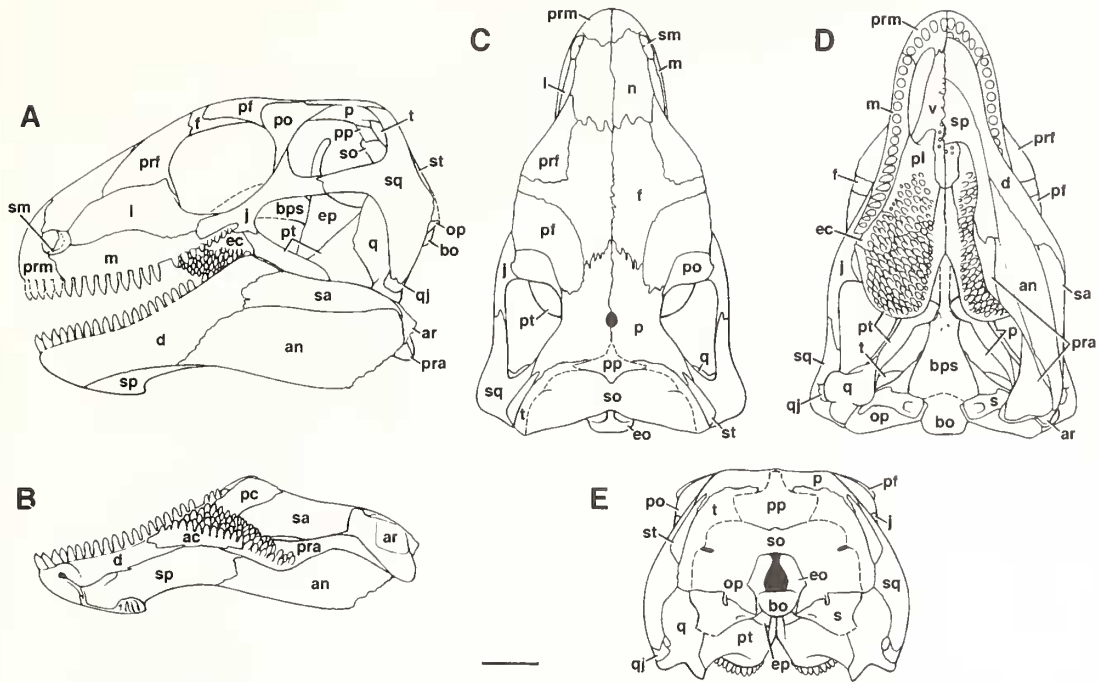
TEXT-FIG. 1. *Edaphosaurus boanerges* Romer and Price 1940. Outline guide to skull reconstructions in Text-figures 2–4. A, skull and left mandible in left lateral view; B, right mandible in medial view; C, skull in dorsal view; D, skull and left mandible in ventral view; E, skull in occipital view. Scale bar represents 20 mm.

opposing dentary teeth become increasingly medially directed; neural spines of the sacral and anterior caudal vertebrae are tall and pointed, with longitudinal ridges running along their lateral surfaces; multiple lateral tubercles, when present, are usually arranged horizontally on the neural spines.

Edaphosaurus boanerges Romer and Price, 1940

Text-figures 1–18

1916 *Edaphosaurus* sp., Williston, p. 233, fig. 81.
1940 *Edaphosaurus boanerges*, Romer and Price, p. 48, fig. 6A; p. 66, fig. 8; p. 79, fig. 12F; p. 86, fig. 15C–D; p. 391, fig. 66.

Diagnosis. A medium-sized *Edaphosaurus* characterized by the presence of 120–150 teeth on each palatal tooth plate and a jaw symphysis that is deeply excavated dorsally; distinguished from other edaphosaurids by the following suite of advanced and primitive characters: frontal lateral lappet slender; anterior presacral neural spines slender; and lateral tubercles slender.

Horizon and Locality. Nocona Formation (formerly Admiral Formation; see Hentz 1988 for stratigraphical review for north-central Texas), Wichita Group, Lower Permian. Study specimens are from the Geraldine Bonebed, approximately 13 km northwest of Archer City, Archer County, Texas.

Holotype. MCZ 1531, a pair of mandibles. According to Romer and Price (1940), this number originally contained 'the remains of about six individuals' from Geraldine, with the type jaws forming part of a mounted

MCZ specimen. In the early 1980s all specimens except the type jaws were reassigned to MCZ numbers 4309–4324.

Study material. MCZ 1680, a partial skeleton with an obliquely compressed skull; MCZ 1762, a partial skeleton with fragmentary skull and mandibles; MCZ 1764, a fragmentary skull; MCZ 4309, a partial skull with mandibles (formerly part of MCZ 1531); ROM 37760, a fragmentary left maxilla. This is not an exhaustive list of *Edaphosaurus boanerges* specimens reposited at the MCZ, ROM, or elsewhere, and includes only those specimens examined here.

Description. The Geraldine specimens permit a confident restoration of the skull of *Edaphosaurus boanerges* (Text-figs 1–4). The reconstruction is based mainly upon MCZ 1762, with additional information taken from
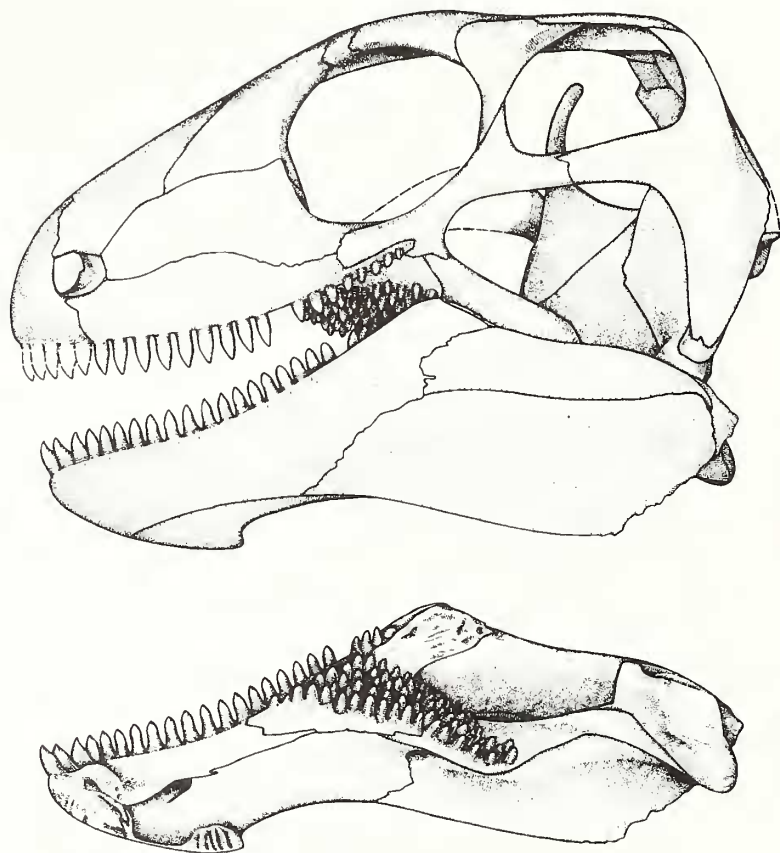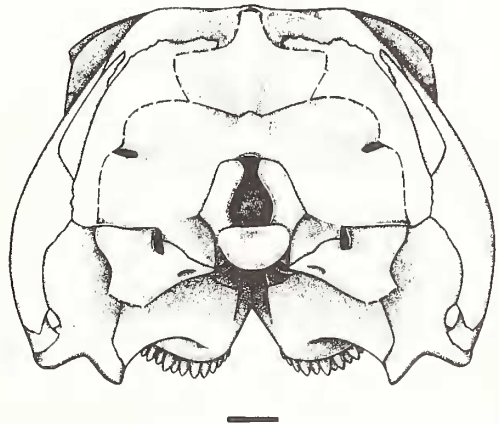

TEXT-FIG. 2. *Edaphosaurus boanerges* Romer and Price 1940. Restoration of skull and left mandible in left lateral view, and right mandible in medial view. Scale bar represents 10 mm.

MCZ 1680, MCZ 1764, and MCZ 4309. The mandible is reconstructed mainly from MCZ 4309, with additional data taken from MCZ 1680 and MCZ 1762. Several features distinguish this genus from other Permo-Carboniferous synapsids. Most significantly, the cheek margin is greatly emarginated, the slender subtemporal bar is displaced dorsally, and the temporal fenestra is enlarged antero-posteriorly. The
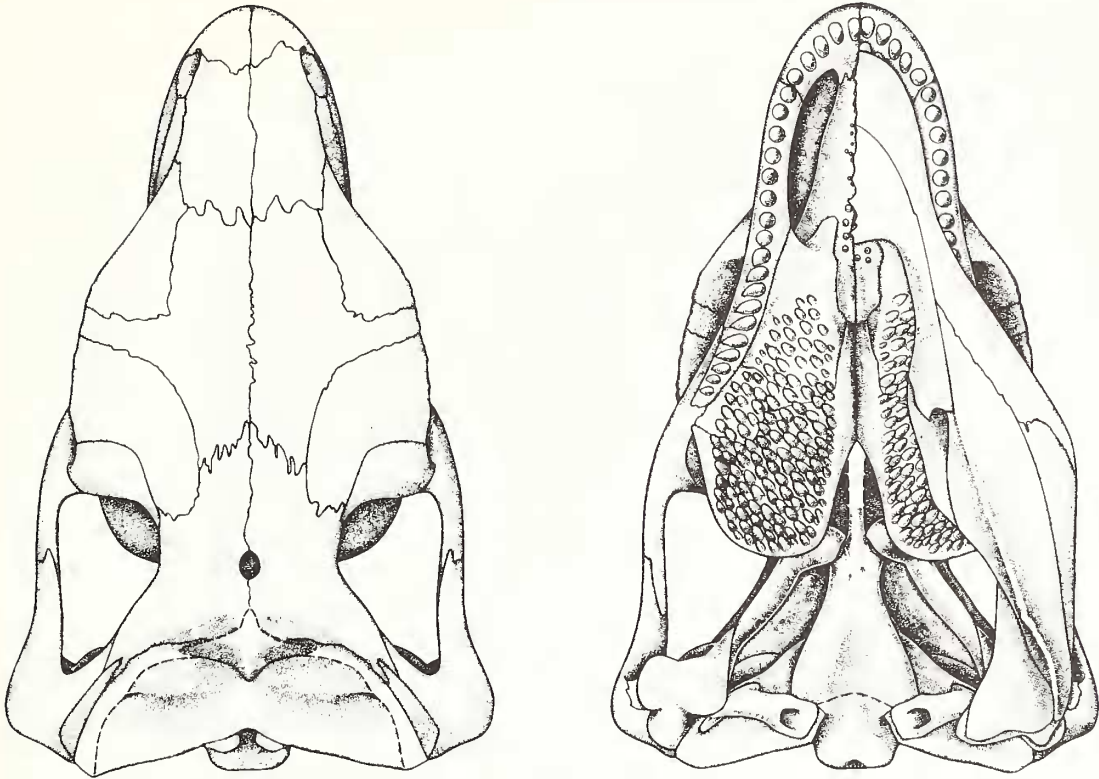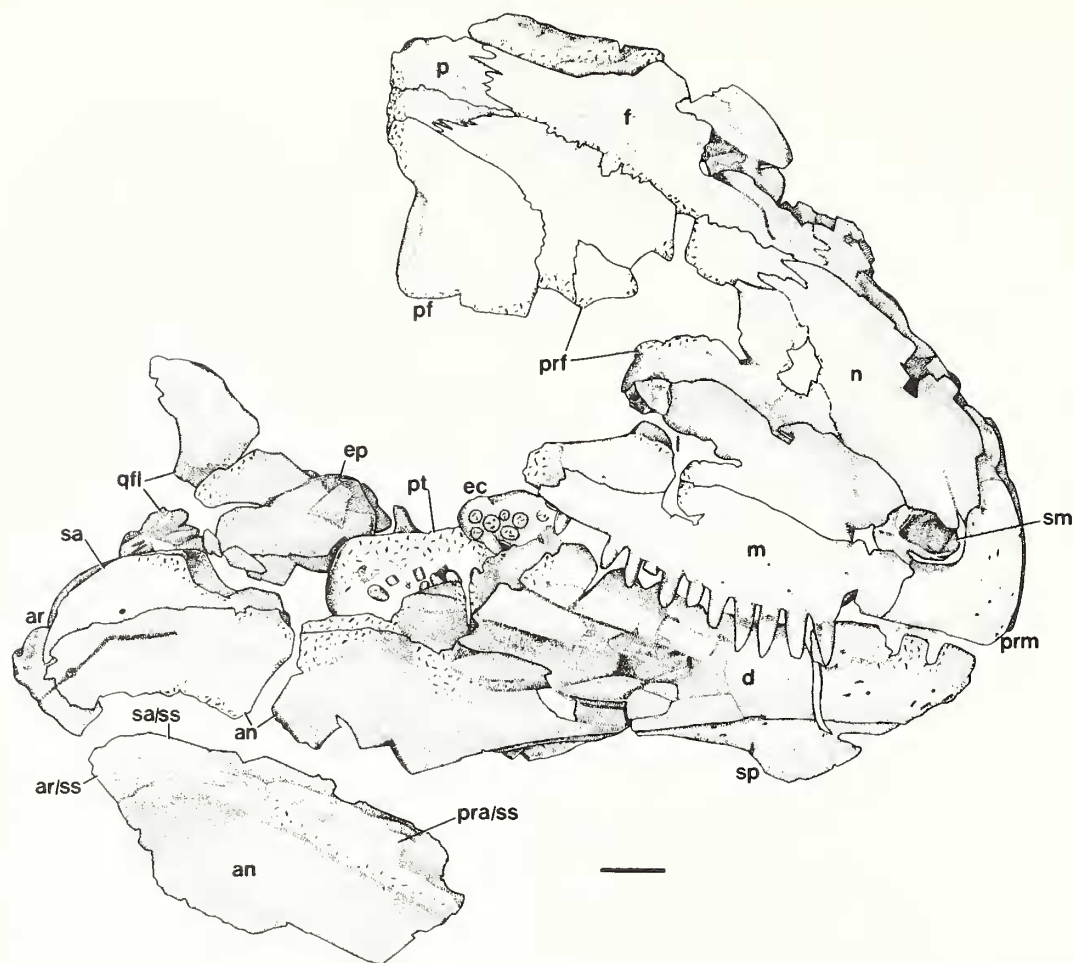
TEXT-FIG. 3. *Edaphosaurus boanerges* Romer and Price 1940. Restoration of skull and left mandible in dorsal and palatal views. Scale bar represents 10 mm.

TEXT-FIG. 4. *Edaphosaurus boanerges* Romer and Price 1940. Restoration of skull in occipital view. Scale bar represents 10 mm.

supraorbital shelf is very deep transversely and conceals the orbits in dorsal view. The posterior maxillary teeth become increasingly laterally directed posteriorly along the marginal tooth row.

Skull. The dorsal process of the premaxilla (Text-fig 5), obliquely elongate in cross section, overlies a broad anterior shelf of the nasal. The vomerine process is not preserved well enough for description. The premaxilla
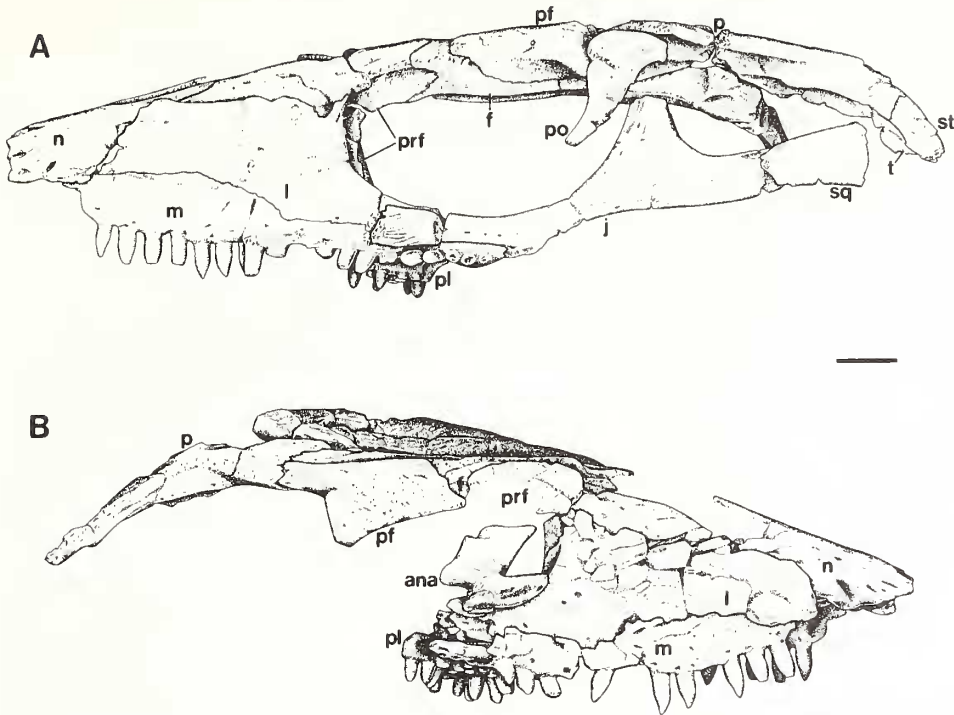
TEXT-FIG. 5. *Edaphosaurus boanerges* Romer and Price 1940; MCZ 1680; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Skull roof and right mandible in right lateral view, and left angular in medial view. Scale bar represents 10 mm.

accommodates five teeth, but none is preserved well enough to determine their length. However, the cross-sectional area of the premaxillary tooth stumps of MCZ 4309 are similar to those of the maxillary dentition, which suggests that the premaxillary teeth probably differed little in size from those of the maxilla.

The septomaxilla (Text-fig. 5) extends the full height of the narial opening, and the medial shelf is large enough to have easily made contact with the nasal septum at the midline. The presence of a posterolateral process on the septomaxilla, seen in sphenacodontids, cannot be determined.

The maxilla (Text-figs 5–7) is a slender rod of bone accommodating 18–21 teeth. All previous descriptions of the marginal dentition of *Edaphosaurus* restored the teeth vertically, as in most other early tetrapods. The well preserved Geraldine materials reveal that the alveolar ridges of the maxillae and dentaries are twisted, such that their posterior teeth become directed laterally and medially, respectively. The lateral edge of the maxillary alveolar ridge becomes disproportionately thinner posteriorly than the medial edge, and the ventral surface of the alveolar portion exhibits a progressive lateral flexure, approximately 13°–16° at the sixteenth tooth position, and roughly 35°–40° at the eighteenth and nineteenth tooth positions. Accordingly, the angle of tooth implantation changes, and the posterior maxillary teeth become increasingly laterally directed. In lateral aspect, the ventral margin of the maxilla is arched weakly, and the lateral edge forms a distinct lip over the tenth

TEXT-FIG. 6. *Edaphosaurus boanerges* Romer and Price 1940; MCZ 1762; Geraldine Bonebed, Lower Permian; Archer Co., Texas. A, left lateral and B, right lateral views of skull. Scale bar represents 10 mm.

through fifteenth teeth. The implantation of the teeth (Text-fig. 9) is protothecodont. Each tooth bears a perceptible shoulder, beyond which it attenuates to a sharp tip. The tips are compressed slightly transversely and curve slightly posteriorly. Posterior cutting edges are aligned slightly posterolaterally, whereas anterior cutting edges are inclined anteromedially. Many teeth feature extremely fine serrations along their cutting edges, and these are emphasized by short, oblique grooves running inwards from the edge; those teeth lacking serrations presumably lost them from heavy use. Approximately every third tooth in the maxillae of MCZ 1762 is at the same level of development, and there are few natural gaps in the marginal dentition, suggesting that tooth replacement was relatively rapid. Wear is present on several anterior teeth in MCZ 1762, occurring as a planing-off of the lingual surface of the shoulder; the posterior teeth are too damaged to determine true tooth-to-tooth wear. However, examination of ROM 37760 reveals that many of the procumbent posterior teeth display similar wear on their lingual surfaces.

In lateral aspect, the lacrimal (Text-figs 5–6, 10) underlies the dorsal flange of the maxilla anteriorly, but as the lacrimal becomes progressively thicker posteriorly, it comes to overlie the maxilla totally. The medial wall of the lacrimal duct is thicker than the lateral wall, perhaps to strengthen contact with the ventral process of the prefrontal medially. The lacrimal is greatly thickened along the orbital margin and has a well-developed contact with the ventral process of the prefrontal.

Anteriorly, the nasal (Text-figs 5–7) has a strongly scarred shelf for the reception of the premaxilla, and the internasal suture is bevelled and irregular, presumably to strengthen the snout against forces generated during feeding.

The ventral process of the prefrontal (Text-figs 5–7) is transversely thick and is attached solidly to the medial surface of the lacrimal. The transverse width of the ventral process decreases ventrally in direct proportion to a progressive increase in the width of the lacrimal, forming a stout buttress of constant width between the skull roof and palate (Text-fig. 10). The ventral process continues dorsally as a ridge on the ventral surface of the posterodorsal process.

Romer and Price (1940) reconstructed the frontal with a large lateral lappet. However, the lateral lappet of the frontal (Text-figs 5-8) is markedly slender, with a lateral exposure about one-quarter that of the
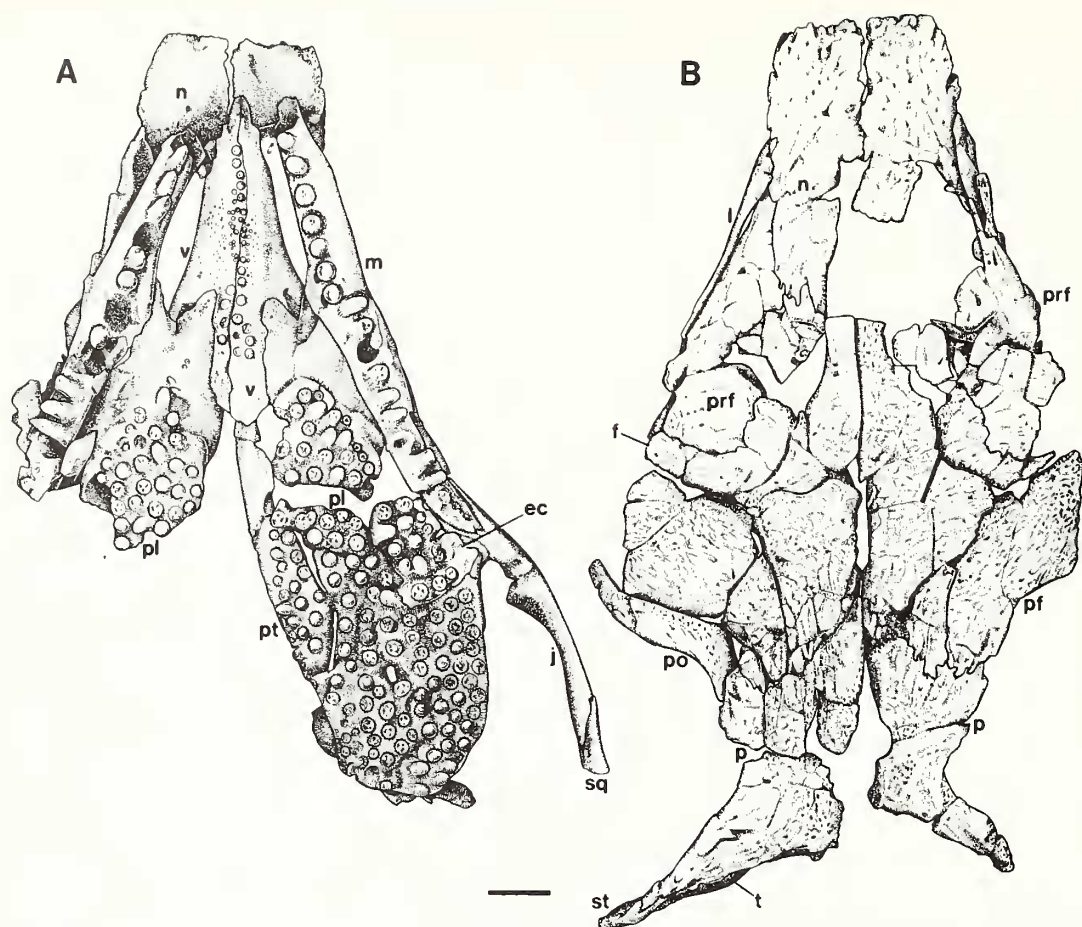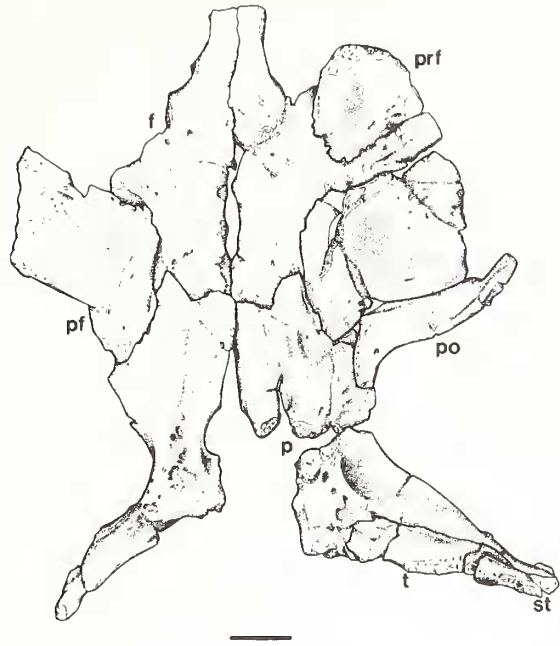
TEXT-FIG. 7. *Edaphosaurus boanerges* Romer and Price 1940; MCZ 1762; Geraldine Bonebed, Lower Permian; Archer Co., Texas. A, palatal and B, dorsal views of skull. Scale bar represents 10 mm.

postfrontal. Posteriorly, the frontal overlies, and has a moderately to deeply serrate suture with, the parietal; a ventral ridge extends anteriorly from this suture to contact and merge with the ventral ridge and ventral process system of the prefrontal.

A notable feature of the parietal (Text-figs 6–8) is its concave lateral edge. Contrary to previous interpretations, the lateral edge of the parietal was free and formed the dorsal margin of the temporal fenestra. The medial half of the ventral surface of the bone is dominated by two well-developed parasagittal ridges. The lateral ridge is continuous with the ventral ridge of the frontal, and presumably marks the former contact of the orbital-plate cartilage, whereas the medial ridge arises immediately anterior to the parietal foramen, extends to the posterior edge of the parietal, and overlies an anterodorsal pilaster-like process of the postparietal. Posteriorly, the parietal has a small occipital shelf that contacts the postparietal and the tabular.

The lateral edges of the postparietal (Text-fig. 11) of MCZ 1762 are imperfectly preserved, making it difficult to establish the precise nature of the contact with the tabular and the parietal. However, scars present on the posterior margin of the parietal suggest that the postparietal overlies the occipital flange of the parietal. A pair of pilaster-like projections arise from a point slightly lateral to the centre of the anterior surface and end dorsally as broad-based supports for the medial ventral rugosities of the parietals. These processes lie snugly within the crenels of the dorsal process of the supraoccipital. A small, median process extends anterodorsally from the postparietal to interpose itself between the posterior ends of the parietals; this is inferred by a small, triangular gap which lies sagitally between the ends of the articulated parietals. An anterodorsal process is found also on the postparietal of *Edaphosaurus pogonias* (AMNH 4009).

TEXT-FIG. 8. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Skull table of MCZ 1762 in ventral view. Scale bar represents 10 mm.
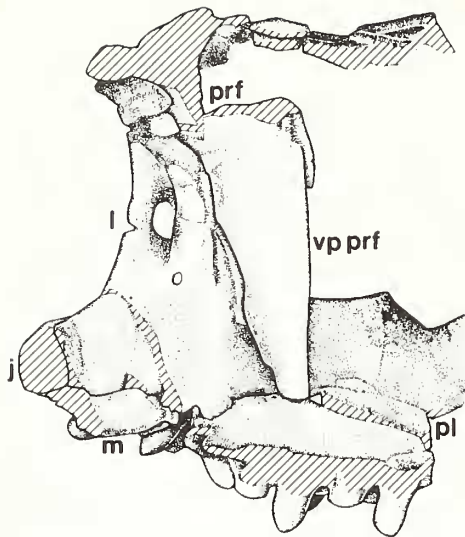

TEXT-FIG. 9. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Maxillary teeth of MCZ 1762. A, occlusal and B, lingual views of 6th and 7th right maxillary teeth; C, lingual view of the tip of unankylosed maxillary tooth, showing serrations. Scale bars represent 1 mm.
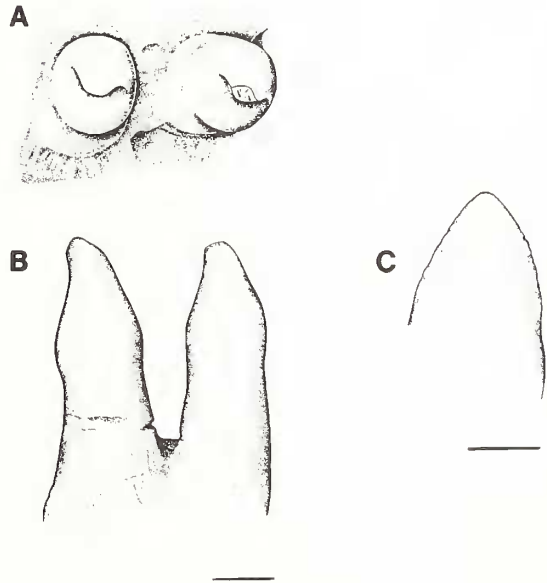
The supratemporal (Text-figs 6–8) is a narrow, gently arched bone with little lateral exposure. The supratemporal of *Edaphosaurus boanerges* differs little from that of *E. pogonias*. The supratemporal of the latter species was reconstructed by Romer and Price (1940) as a large element, but re-examination of the holotype reveals that it, too, is a slender, predominantly occipital element.

The relatively thick dorsal edge of the tabular (Text-figs 6–8) occupies a broad embayment in the posterior edge of the parietal. Though the ventromedial edge of the tabular is not preserved, the preserved parts of the bone rapidly thin inwards from the dorsal edge, suggesting that the ventromedial edge was quite thin. Sutural surfaces on the occipital surfaces of the paroccipital process and lateral process of the supraoccipital mark its ventromedial limits.

TEXT-FIG. 10. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Left antorbital region of MCZ 1762 in posterior view. Hachure indicates broken surface. Scale bar represents 10 mm.
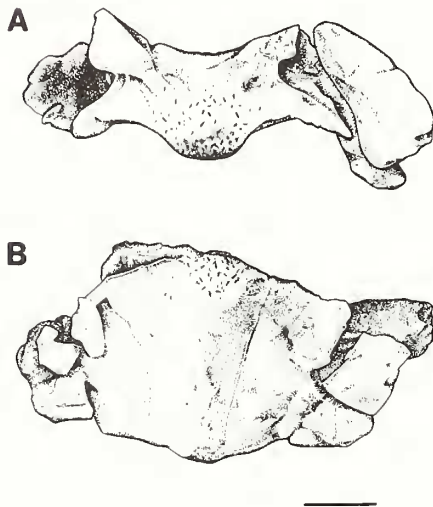
TEXT-FIG. 11. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Postparietal of MCZ 1762. A, dorsal and B, posterior views. Scale bar represents 5 mm.

The postfrontal (Text-figs 5–8) consists of a small but thick posterior process that gives rise to a wedge-shaped anterior flange that forms the posterior half of the supraorbital hood. The sutural surface for the postorbital is twisted: internally and medially the posterior process of the postfrontal overlies the base of the postorbital posterior process, whereas laterally it underlies the postorbital.

The postorbital (Text-figs 6–8) is a slender, sigmoidal bone. The posterodorsal process does not extend posteriorly beyond the pineal foramen, and it is completely overlain by the parietal. In spite of the fragmentary nature of the available squamosals, it is very unlikely that the postorbital contacted the squamosal. The posterodorsal process does not possess an area that may be interpreted as a sutural surface for the squamosal, nor does the parietal immediately posterior to the postorbital bear any markings for the reception of the squamosal.

The jugal (Text-figs 6–7) is remarkably slender in lateral view, and is laterally compressed for most of its length except for the slightly swollen anterior third. A short protuberance extends medially from the anterior jugal process to contact the palate. The sutural surface for the squamosal is extensive and marked by strong ridges and furrows.

TEXT-FIG. 12. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Palatoquadrate ossifications and associated elements of MCZ 1762. A, medial and B, lateral views. Scale bar represents 10 mm.
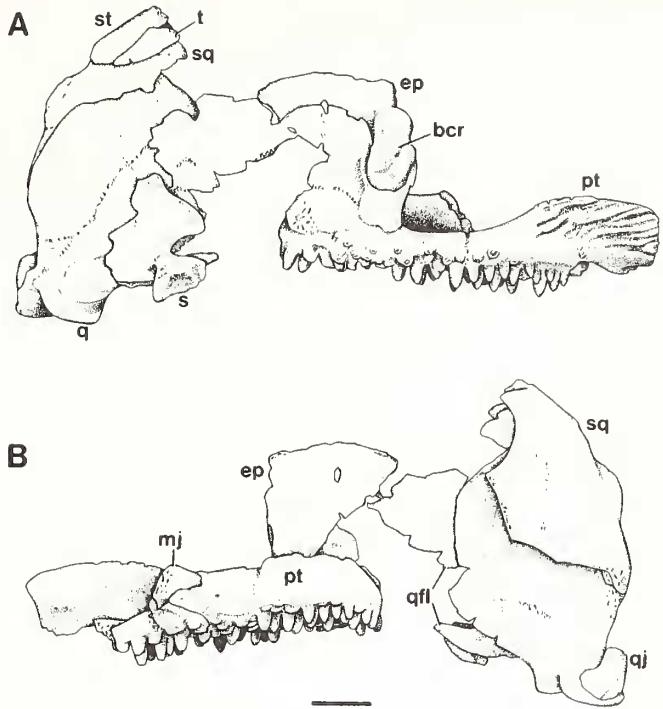
TEXT-FIG. 13. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Left squamosal of MCZ 1680. A, lateral and B, medial views. Scale bar represents 10 mm.
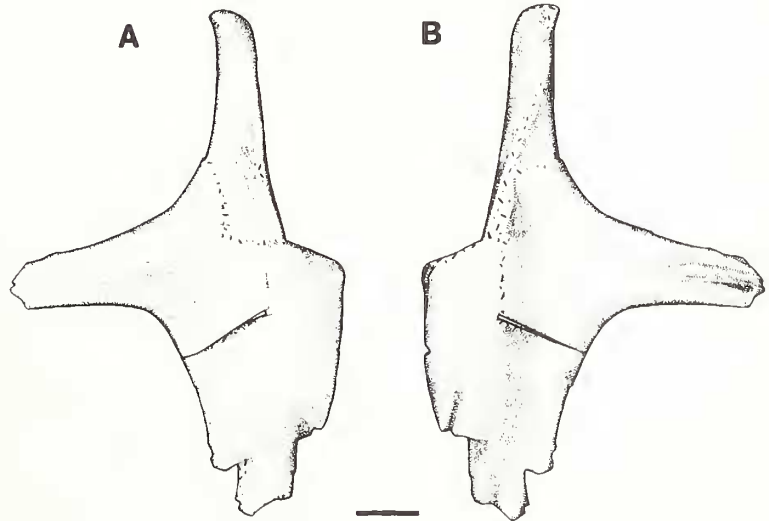
The ventral process of the squamosal (Text-figs 6, 12–13) is well developed. An occipital flange extends medially from the ventral process of the squamosal, and serves as a broad base for the supratemporal and, to a lesser extent, the tabular. A thickened, irregular prominence on the medial edge of the squamosal marks the area receiving the tip of the paroccipital process. The anterior process displays either a slight anteroventral curvature, as in MCZ 1762, or extends forward without arching, as in MCZ 1680.

Despite the absence of well preserved specimens, Romer and Price (1940) described the quadratojugal as extending anteriorly under the postorbital bar. However, the quadratojugal (Text-fig. 12) is antero-posteriorly short and covered laterally by the squamosal, resembling closely those of sphenacodonts.
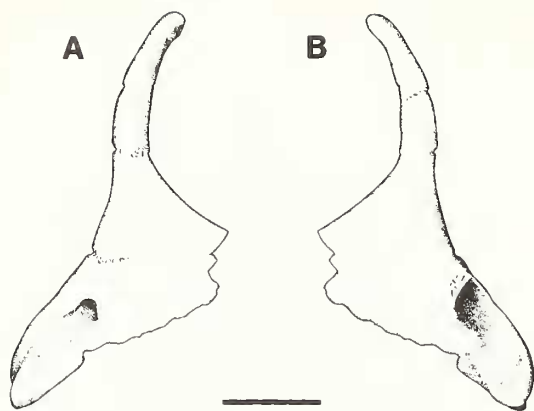
TEXT-FIG. 14. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Left epipterygoid of MCZ 1764. A, lateral and B, medial views. Scale bar represents 10 mm.

The palate departs from the typical primitive synapsid condition in the possession of a pair of large tooth plates, formed by the palatine, ectopterygoid, and pterygoid. These plates are tilted ventrolaterally, are faintly concave in order to meet more firmly the gently convex tooth plates of the mandible, and accommodate about 120–150 teeth each. The internal nares (Text-fig 3) are more elongate than suggested by Romer and Price (1940), but they are neither as long, nor as transversely constricted, as in carnivorous eupelycosaurs. The median longitudinal depression between the tooth plates is deep and compressed transversely, and the post-plate region is significantly more abbreviated than in other genera.

The ventrolateral surface of the vomer (Text-fig. 7) is slightly concave and covered by a shagreen of tiny teeth, which is replaced anteriorly by a smooth surface ingrained by shallow striae. The largest vomerine teeth reach a maximum diameter equal to approximately one-half that of an average-sized plate tooth.

The palatine's (Text-figs 6–7) contribution to the tooth plate is a thick, diamond-shaped structure which bears approximately thirty-two conical teeth. The majority of the teeth are approximately one-half as long and two-thirds the diameter of the maxillary dentition. They are roughly uniform in diameter and are densely packed. Smaller teeth, some approaching the size of the vomerine teeth, occupy the lateral and anterior fringes of the tooth-bearing area. All well-preserved palatal teeth display some degree of wear, which generally takes the form of a planing-off of the tips of the teeth. However, the tips of most teeth appear to have been planed off by previous preparators, making it difficult to identify true tooth wear. A diagonally-orientated orbitonasal ridge arises on the dorsal surface near the lateral edge of the palatine, forms the medial wall of the lateral orbitonasal foramen, and runs anteromedially to the medial orbitonasal foramen. Laterally, the orbitonasal ridge has a small contact with the lacrimal and the ventral process of the prefrontal.

The ectopterygoid (Text-figs 5, 7) is a small element that is almost completely covered ventrally by about fifteen teeth. Laterally, the ectopterygoid has a small contact with the jugal.

The pterygoid (Text-figs 5, 7, 12) is the largest and most complex palatal element. The low dorsal lamina of the pterygoid is scarred medially with numerous longitudinal ridges and grooves, presumably required to withstand the forces generated by the jaw adductor musculature. The ventral surface of the palatal ramus is covered completely by teeth except for the edges bordering the interpterygoid vacuity and the jugal. The tooth plate faces slightly rostrally as well as anterolaterally, and lies well below the level of the cheek in lateral aspect. Nearly 100 teeth are present, and these are set deeply into the alveolus of the tooth plate. The thin quadrate ramus of the pterygoid is similar to those of sphenacodontids, but differs strongly from other eupelycosaurs in the elaboration of the region associated with the epipterygoid. The ramus rises directly upwards from the dental plate and wraps around the basicranial process of the epipterygoid. A broad, prominent channel of unknown function issues from the scrolled flange enclosing the basicranial process and ends abruptly on the dorsal surface of the palatal plate.

The basal portion of the epipterygoid (Text-figs 12, 14) overlies the quadrate ramus of the pterygoid in lateral view. The basicranial process extends medially from the basal portion and ends in a tall, screw-shaped recess for the basipterygoid process of the basiparasphenoid. The ventral half of the recess faces slightly posteriorly as well as medially, whereas the dorsal half faces anteromedially. The basicranial process is held firmly within the anterior fold of the quadrate ramus of the pterygoid. The dorsal columella is a slender, transversely compressed finger of bone that arches posteriorly.

The dorsal and posterior margins of the vertical plate of the quadrate are thickened and flare slightly laterally (Text-fig. 12). The posterior margin has a strong contact with the squamosal and a smaller sutural surface for
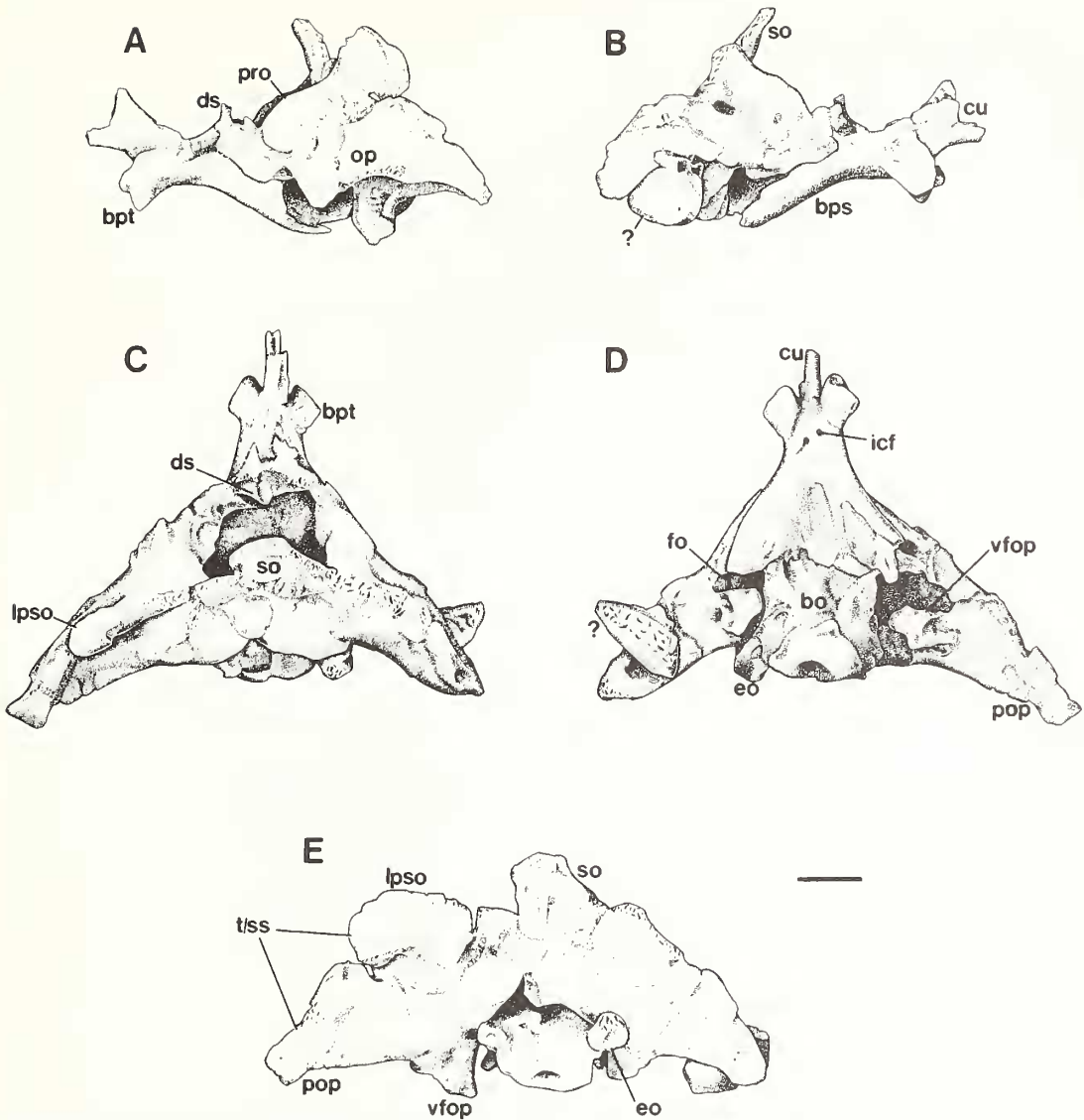
TEXT-FIG. 15. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Braincase of MCZ 1762. A, left lateral, B, right lateral, C, dorsal, D, ventral, and E, occipital views. Scale bar represents 10 mm.

the quadratojugal. A shallow, rounded depression posteromedial to the quadrate foramen probably received the distal end of a cartilaginous extension of the stapes. The two condyles are aligned parasagittally, are separated by a deep notch, and share a single articulating surface.

The braincase (Text-fig. 15) resembles in most respects that of sphenacodontids, but differs in the morphology of the paroccipital processes and the organization of the region formerly surrounding the pituitary body. As in most early synapsids, there is a marked tendency towards fusion of the elements: the parasphenoid and the basisphenoid are united, the supraoccipital is fused to the opisthotics and the proötics, and the basioccipital and exoccipitals are fused.

Because the basisphenoid and its dermal cover, the parasphenoid, are indistinguishably fused, the term basiparasphenoid is used here when referring to this complex. The cultriform process is poorly known, but
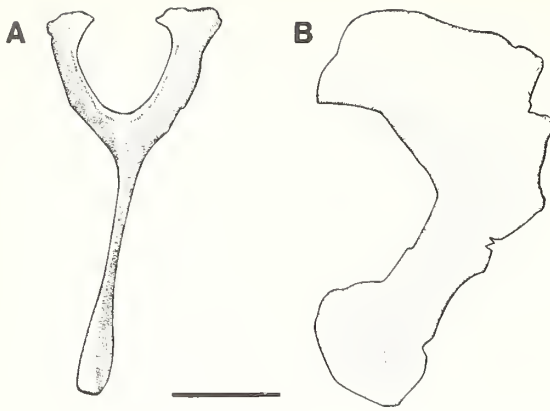
what is preserved indicates that it projected forward from the anterior end of the bone as a narrow trough. The bifaceted basipterygoid processes extend anterolaterally from the complex. Each has a prominent hourglass-shaped articulating surface, with a dorsal facet directed posterolaterally, and a marginally larger ventral facet orientated anterolaterally. Immediately posterior to the dorsal basipterygoid demi-facets, the lateral walls of the basiparasphenoid of MCZ 1762 have been pushed inwards revealing the underlying vidian canals. Crushing makes it difficult to determine the suture with the proötics. Ventrally, the basal tubera contacted the ventral margins of the proötics and the stapedial footplates.

The longitudinal trough of the sphenethmoid (Text-fig. 16) is open dorsally; the dorsal edges of the trough feature distinct lips that project medially, but these do not appear to have been interconnected by cartilage, as their edges are smoothly finished. The well preserved posterior edge is strongly sigmoidal, as in other forms in which this bone is known. Unfortunately, the anterior portion of the element is missing, and it is impossible to determine how far anteriorly the bone extended.

The proötics (Text-fig. 15) form the relatively gracile dorsum sella. The dorsum sella is poorly preserved in MCZ 1762, but what is present suggests that it resembles a thin, posteriorly-arching wall, which differs significantly from the thick, plate-like structures of other early synapsids. As in sphenacodontids (Romer and Price 1940), the proötic forms the anterolateral wall of the otic capsule, but the free dorsal border is smooth, rounded, and is considerably longer than those described for sphenacodontids (Romer and Price 1940; Eberth 1985).

Each opisthotic (Text-fig. 15) contacts the basiparasphenoid on either side of a deep, ventral emargination representing the lateral margin of the ventral opening of the otic capsule. A ventral flange extends ventrally, abuts the basioccipital tubercle, and marks the posterior edge of the fenestra ovalis. The paroccipital process extends slightly ventrally as well as posterolaterally, and terminates with a blunt, downturned tip. A pronounced ridge at the base of the process on the anteroventral edge abutted the anterior edge of the stapedial dorsal process, and immediately posterior to the ridge lies an elongate scarred area for the reception of the dorsal process of the stapes.

Dorsally, the supraoccipital (Text-fig. 15) lies just below the upper edge of the postparietal, and its unfinished dorsal edge is crenellated for the accommodation of the pilaster-like processes of the latter. Light scarring on the lateral processes marks the sutural surface for the tabular.

The dorsal tips of the exoccipitals constrict slightly the dorsal part of the foramen magnum. The dorsal edge of the shallow notochordal pit on the occipital condyle probably marks the ventral extent of the exoccipitals, and a pronounced median ridge along the floor of the braincase of MCZ 1762, exaggerated by crushing, marks the line of contact between the fused exoccipitals. The basioccipital forms most of the semicircular occipital condyle. The articulating surface of the condyle is separated from its neck by narrow ridges, and a medial ridge, more strongly developed than that seen in sphenacodontids, arises from the ventral lip of the condyle and merges anteriorly with the body of the basioccipital. Paired basioccipital tubera, arched strongly ventrally in parasagittal section, extend laterally to contact the ventral flanges of the opisthotics.

The stapes (Text-fig. 12) is similar to that of sphenacodontids (Romer and Price 1940; Eberth 1985). The dorsal process widens above the footplate, and has a strongly convex lateral margin, which is slightly thinner than the medial edge. The quadrate process is blade-like rather than rod-like as described by Romer and Price (1940). It ends in unfinished bone, and was probably tipped with cartilage. The stapedial foramen is large

relative to the size of the footplate, as two small, thin sheets couple the body to the footplate. The footplate is oval in medial view, with the long diameter aligned parallel to the axis of the stapedial foramen.

Mandible. Relative to its length, the mandible of *Edaphosaurus* (Text-figs 2–3) is much deeper than those of other eupelycosaurian genera. The symphysis can be subdivided into a large, anterodorsal pad and a smaller, posteroventral pad. A large denticulate plate occupies the central third of the lingual surface, and accommodates approximately sixty teeth that are indistinguishable from those of the palatal plates. The tooth plate does not extend as far forward as restored by Romer and Price (1940). The alveolar ridge of the dentary is twisted posteriorly, causing the posteriormost marginal teeth to become medially directed. Except for the vertically aligned angular keel, the jaw leans laterally.
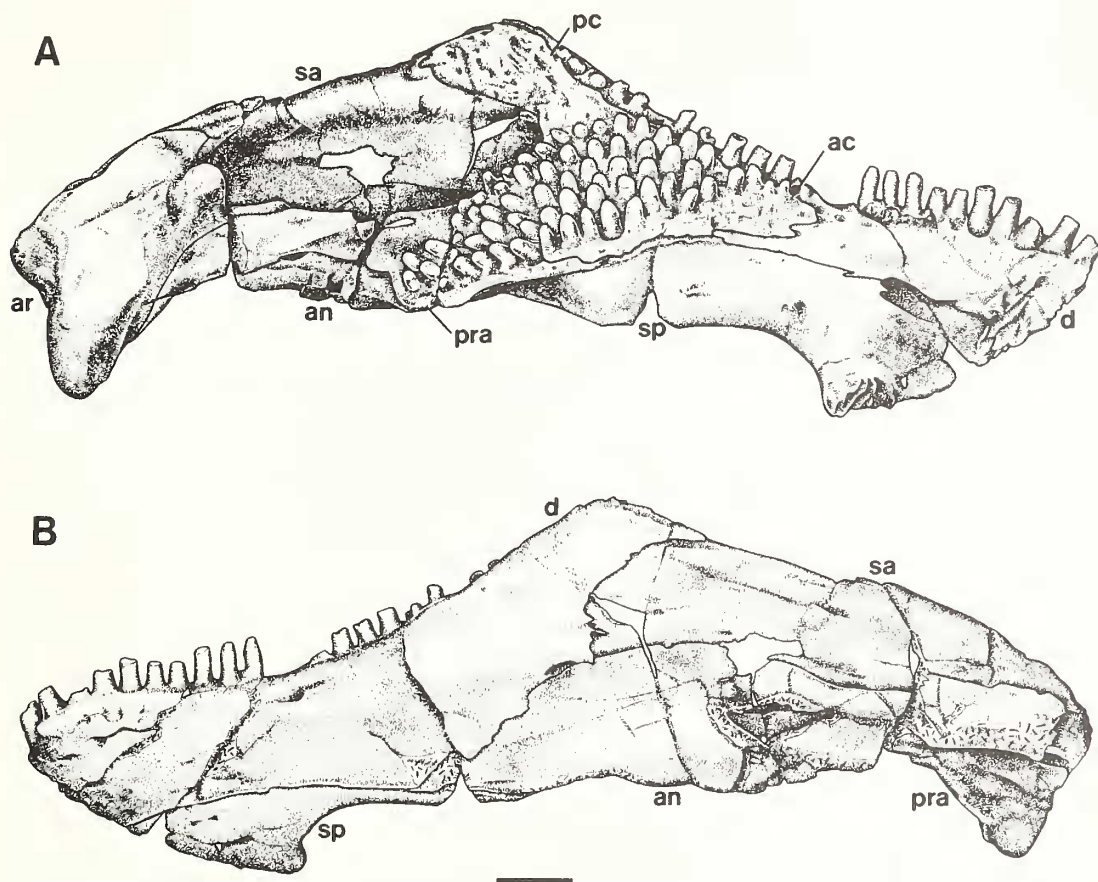
TEXT-FIG. 17. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Left mandible of MCZ 4309. A, medial and B, lateral views. Scale bar represents 10 mm.

The dentary (Text-fig. 17) occupies the anterior 70 per cent. of the mandible in lateral view. It forms most of the anterior symphyseal pad, but makes no contribution to the smaller posterior pad. The anterior pad is incised deeply by an anterior extension of the meckelian canal. Posteriorly, the dentary contacts the angular and surangular with a serrate, overlapping suture, and forms the lateral portion of the angular coronoid eminence. The dentary accommodates about 23 tall, isodont teeth, which, except for their slightly smaller size, resemble those of the upper marginal dentition. The alveolar ridge of the dentary is twisted inwards posteriorly, such that the most posterior marginal teeth lean lingually. Unfortunately, the surfaces of most teeth are damaged, but the orientation of wear present on the labial surfaces of the recumbent teeth suggests that they contacted the upper dentition.

Anteriorly, the splenial (Text-fig. 17) extends downwards and medially as a prominent symphyseal flange, which contacts its fellow at the midline. The anterior half of the symphyseal flange of the splenial is exceedingly thin, such that a pocket lies dorsally between the anterior and posterior symphyseal pads. This condition differs from that seen in *Edaphosaurus pogonias* (AMNH 4009) and *Dimetrodon*, in which the symphyseal area consists of a single large pad. Although the symphyseal flange of the splenial does extend farther ventrally than in other eupelycosaur taxa, it is not as extensive as reconstructed by Romer and Price (1940), as they have apparently restored the mandible vertically. The mandible displays, instead, a strong lateral lean, which foreshortens the lateral exposure of the splenial. Posteriorly, the splenial becomes twisted almost 90° beneath the medially expanded tooth plate, and its posterior edge forms the anterior margin of the caudally-directed inframeckelian foramen.

The anterior coronoid (Text-fig. 17) is moderately arched dorsally and accommodates approximately sixteen teeth. Most of the bone overlies the posterior end of the splenial, but anteriorly and posteriorly it has smaller contacts with the dentary and prearticular, respectively. The posterior coronoid (Text-fig. 17) is a typically triradiate structure. The ventral half supports a dense field of about forty isodont, peg-like teeth. The tooth field is approximately four tooth bases wide, but the teeth are not arranged in true rows as in some multiple-tooth rowed captorhinids, as they are irregularly positioned. In ventromedial view, the tooth field is dorsally arched. The tips of several teeth bear oblique facets, which may represent true tooth wear. The superior half of the posterodorsal process is etched deeply by a system of vermiculate grooves, and its dorsal rim bears deep pits and a strong spur, for the insertion of the jaw adductor musculature.

The prearticular (Text-fig. 17) forms most of the floor of the adductor fossa. Its anterior third is expanded medially and accommodates nine teeth. The prearticular overlies a long medial shelf of the angular, but posteriorly this contact becomes attenuated and eventually disappears as the prearticular becomes more closely associated with the articular, where the prearticular becomes exceedingly thin and twisted, and sheathes the ventral face of the pterygoideus process of the articular.

The dorsal margin of the surangular (Text-fig. 17) is moderately arched laterally. It is notably thickened dorsally, but becomes thinner ventrally. Anteriorly, the surangular is sandwiched between the posterodorsal processes of the posterior coronoid and dentary, and the dorsal margin bordering the posterior coronoid is deeply scarred, demonstrating that the M. adductor mandibulae externus extended at least this far posteriorly onto the surangular.

The angular (Text-figs 5, 17) is the second largest bone in the mandible. A medially-projecting shelf buttresses the prearticular and forms the ventral margin of the inframeckelian foramen. Ventrally, a deep, vertical keel extends downwards from the body of the angular, and becomes thinner in cross-section distally. The edge of the keel is smoothly finished anteriorly, but the posterior third is thickened and slightly crenulated, which suggests that the edge of the keel may have served as the site of insertion for musculature of uncertain origin. The posterior third of the keel is arched slightly laterally, possibly to allow the pterygoideus musculature to insert on the ventral surface of the pterygoideus process.

The articulating surface for the condyle of the quadrate dominates the dorsal surface of the articular (Text-figs 5, 17–18) and is approximately 50 per cent. longer in antero-posterior dimension than the articulating
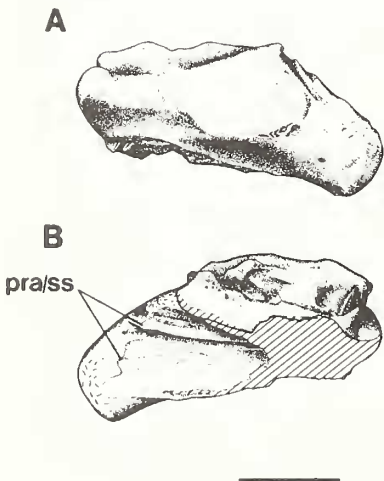

TEXT-FIG. 18. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Right articular of MCZ 1762. A, medial and B, ventrolateral views. Hachure indicates broken surface. Scale bar represents 10 mm.

surface of the opposing quadrate. The inward-tilting surface consists of two main elliptical areas divided by an antero-posteriorly directed ridge which fits into a notch in the quadrate. The ridge continues anteriorly and swells into a large, anterior boss. The anterior process of the articular extends forwards along the floor of the adductor fossa between the surangular and prearticular and narrows anteriorly, ending in unfinished bone that presumably continued forwards as cartilage. A robust retroarticular process projects backwards and bears numerous fine ridges and furrows for attachment of the M. depressor mandibulae. In contrast to the reconstruction of the mandible by Romer and Price (1940), the pterygoideus process of the articular projects posteriorly as well as ventromedially. Its posterodorsal surface is marked by pits and grooves, which suggests that the pterygoideus musculature may have inserted at least this far posterodorsally on the process. A longitudinal groove, presumably the chorda tympani canal, traverses the sutural surface for the prearticular (Text-fig. 18).

<div align="center">DISCUSSION</div>

Phylogenetic relationships

The family Edaphosauridae occupies a prominent phylogenetic position among early synapsids as the sister group to Sphenacodontia (*sensu* Reisz *et al.* 1992), the Permo-Carboniferous clade which eventually gave rise to mammals. The relationships of Edaphosauridae to other basal synapsid groups is given in Text-figure 19A.
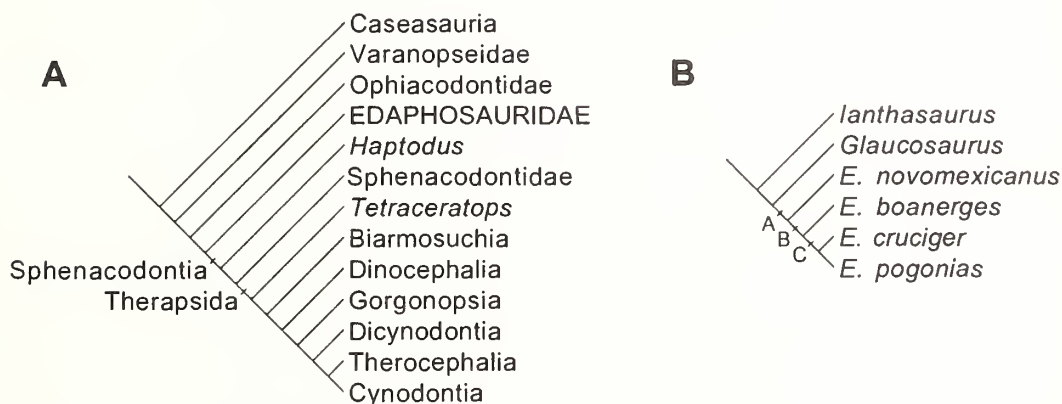
TEXT-FIG. 19. Phylogenetic trees discussed in the text. A, cladogram showing the phylogenetic position of Edaphosauridae among Palaeozoic Synapsida. Adapted from Rowe (1988), Laurin and Reisz (1990), and Reisz *et al.* (1992). B, cladogram illustrating a hypothesis of edaphosaurid interrelationships. See text for synapomorphies diagnosing nodes A–C.

Edaphosauridae is comprised currently of three genera and nine species from the Permo-Carboniferous of North America and Europe (Reisz 1986; Modesto 1994). Seven edaphosaurid species are assigned to the genus *Edaphosaurus*. However, the assignment of two European species to the genus has been questioned because of the fragmentary nature of their respective holotypes (Reisz and Berman 1986; Modesto and Reisz 1990). Although based upon only fifteen morphological characters, a tentative phylogeny for edaphosaurids presented by Modesto and Reisz (1992) corroborated previous hypotheses concerning interrelationships among the better known species of *Edaphosaurus* (Romer and Price 1940; Reisz and Berman 1986). The Geraldine *E. boanerges* cranial material described here allows for the reinterpretation of the cranial anatomy of other members of the genus. Accordingly, this permits a phylogenetic analysis of *Edaphosaurus* more comprehensive than heretofore possible.

The following edaphosaurid taxa, including *Edaphosaurus boanerges*, form the ingroup: *E. novomexicanus*, from the Permo-Carboniferous of New Mexico, redescribed recently by Modesto and Reisz (1992); the two largest edaphosaurids, *E. cruciger* and *E. pogonias*, from the Lower

Permian of Texas, known adequately from early descriptions (Case 1907; Romer and Price 1940) with both cranial and postcranial material examined by the author. In addition to the cranial information presented in this paper, the postcranial osteology of *E. boanerges* is known from a description by Romer and Price (1940).

Due to their fragmentary nature, three taxa are omitted from the analysis: *Edaphosaurus colohistion*, from the Lower Permian Pittsburgh Formation of West Virginia, excluded as it is known only from a single series of presacral vertebrae and dorsal ribs (Berman 1979); similarly, two small European taxa assigned to the genus (Reisz 1986) are omitted.

The following taxa serve as outgroups: *Ianthasaurus hardestii*, from the Upper Pennsylvanian of Kansas (Reisz and Berman 1986; Modesto and Reisz 1990), and *Glaucosaurus megalops*, from the Lower Permian of Texas and identified recently as an edaphosaurid (Modesto 1994), represent the small, presumably carnivorous, members of the family; *Haptodus garnettensis* (Laurin 1993) and the varanopseid *Mycterosaurus* (Berman and Reisz 1982) serve as more distant outgroups.

Thirty-six characters were used in the analysis. These are described in Appendix 1. Many of these are from the literature (Romer and Price 1940; Brinkman and Eberth 1983; Modesto and Reisz 1992), although a few are new. The analysis was run on a Macintosh Quadra 800 computer using the branch-and-bound algorithm of PAUP 3.1, which is guaranteed to find the most parsimonious trees. Character states were optimized using the delayed transformation (DELTRAN) algorithm and run unordered.

The most parsimonious tree (Text-fig. 19B) requires 38 steps and has a consistency index of 0·973. Synapomorphies are grouped below under the nodes and/or the taxonomic units that they diagnose. Numbers appearing in square brackets refer to character descriptions listed in Appendix 1; multiple character states, indicated as 1 or 2, are encased in parentheses. A negative sign indicates a reversal, and asterisks denote ambiguous characters, which may define more inclusive nodes.

Node A. The following synapomorphies diagnose *Edaphosaurus*: 1. marginal teeth slightly bulbous [1]; 2. alveolar ridges twisted [7]; 3. supraorbital margin expanded laterally [10]; 4. parietal lateral margin deeply concave [11*]; 5. quadrate condylar portion saddle-shaped [14*]; 6. jaw suspension offset ventrally [15*]; 7. skull short [16*]; 8. postorbital and antorbital regions subequal [17*]; 9. tooth plates present [19]; 10. cervical centra short [23*]; 11. neural arches not excavated [-28*]; 12. dorsal vertebrae with elongate transverse processes [29*]; 13. sacral and caudal neural spines with rugose tips [30*]; 14. sacral and caudal neural spines with longitudinal ridges [31*]; 15. caudal neural spine tips expanded sagitally [32*]; 16. caudal neural spines tall and pointed [33*]; 17. dorsal ribs strongly curved [34*]; 18. dorsal rib tubercula greatly reduced [35*].

Node B. These apomorphies diagnose the clade of Texan edaphosaurids, *E. boanerges*, *E. cruciger*, and *E. pogonias*: 1. marginal teeth with cutting edges [2*]; 2. frontal lateral lappet slender [9]; 3. postorbital does not contact squamosal [12*]; 4. mandible short and deep [20*]; 5. splenial lateral exposure enlarged [22*]; 4. ilium with well-developed anterodorsal process [36(2)*].

Node C. These apomorphies diagnose the clade of *E. cruciger* and *E. pogonias*: 1. dentary anteroposterior length equal to or less than two-thirds of mandibular length [21]; 2. swollen-tipped lateral tubercles present [26(2)]; 3. club-shaped anterior presacral neural spines [27].

Eighteen apomorphies diagnose the genus *Edaphosaurus*. Three of these are newly identified *Edaphosaurus* synapomorphies: the twisting of the alveolar ridges [7]; the saddle-shaped quadrate condyle [14]; and the absence of lateral excavations on the neural arches [28]. However, five of the six apomorphies diagnosing the clade of Texan edaphosaurs are ambiguous since they cannot be determined in *E. novomexicanus*, and therefore may represent additional synapomorphies of the genus. Similarly, many of the apomorphies diagnosing *Edaphosaurus* are ambiguous, due to the total absence of postcrania of *Glaucosaurus megalops*. It is possible that analysis of new material attributable to this little edaphosaurid may unite it more strongly to *Edaphosaurus*. The presence of serrations on the marginal teeth, the oblique arrangement of the cutting edges of the marginal teeth, the presence of a medial process on the jugal, the anterior folding of the quadrate flange of

the pterygoid, and the presence of a posterior infra-meckelian foramen, all present in *E. boanerges*, but not currently determinable in other members of the genus, may represent further synapomorphies of *Edaphosaurus*. In the course of compiling the data matrix, two characters used formerly to diagnose this genus were found to be of limited use. The first, reduced marginal dentition (Reisz 1986; Reisz and Berman 1986), is difficult to assess, since eupelycosaurian tooth counts cannot be separated into discrete categories for the purposes of character-state coding. In any event, *Glaucosaurus megalops* possesses fewer marginal teeth than *Edaphosaurus*. The second problematical character, the presence of an ectepicondylar foramen (Romer and Price, 1940; Reisz 1986), can be determined only in *E. boanerges* and *E. pogonias*.

   Edaphosaurus boanerges, *E. cruciger*, and *E. pogonias* form a clade, with the latter two species being more closely related to each other than either is to *E. boanerges*. Romer and Price (1940) suggested tentatively that these species may have formed a species phylum, since *E. cruciger* appears to replace *E. boanerges*, and *E. pogonias* in turn appears to replace *E. cruciger* in regular succession in the Wichita and Clear Fork deposits; the sequence would be among the earliest of examples of anagenesis in Amniota. However, the Texan edaphosaurids demonstrably do not form a species phylum, as each possesses at least a single autapomorphy. *Edaphosaurus pogonias* is distinguished among Permo-Carboniferous synapsids in possessing two spade-like dorsal processes on the ilium. Its sister taxon *E. cruciger* is distinguished by one autapomorphy, the anterior margins of the clavicular plate and the clavicular stalk describe a distinct angle in anteroventral view (personal observation of AMNH 4060); the same edges on the clavicles of the other species of *Edaphosaurus* form a continuous, concave margin. *Edaphosaurus boanerges* possesses two autapomorphies: (1) the palatal tooth plates of this species possess 20–50 per cent. more teeth than those of other *Edaphosaurus* species for which tooth-plate tooth counts can be determined; and (2) the jaw symphysis is deeply excavated dorsally. However, these autapomorphies are currently ambiguous, because these characters are indeterminable in the single skull assigned to *E. cruciger*.

Diet and feeding system

The superb quality of the *E. boanerges* cranial material warrants a re-examination of the adaptation to herbivory that has long been attributed to *Edaphosaurus*. Although the genus possesses many features that are shared with other early herbivores, Williston (1914) had misgivings that *Edaphosaurus* was herbivorous, and later postulated a diet of (unspecified) invertebrates (Williston 1916). Case (1918) believed that the morphological evidence available at the time was equivocal, and considered *Edaphosaurus* to have been either exclusively molluscivorous or exclusively herbivorous. Both hypotheses were prompted by the presence of tooth plates on the palate and the inner aspect of the mandible. Romer and Price (1940) concurred with Case's (1918) second hypothesis, remarking that fossils of freshwater molluscs are absent from the terrestrial deposits that have produced *Edaphosaurus* specimens, and added that a large, barrel-shaped rib cage is found only in herbivorous reptiles. However, the adaptation to herbivory in *Edaphosaurus* has been questioned recently (Munk and Sues 1993), and it is therefore necessary to review the evidence supporting the hypothesis of herbivory in this genus.

   In addition to the presence of the tooth plate dental batteries and the barrel-shaped body, there are several other, non-dental features mentioned briefly by Romer and Price (1940) and subsequent authors (Olson 1986; Reisz 1986) that lend support to the herbivory hypothesis, largely because they are found also in other herbivorous forms and are not present in carnivorous taxa. These include small skull size, isodonty, reduced marginal tooth number, the abbreviated antorbital region, enlarged temporal fenestrae, the ventral offsetting of the jaw suspension, and antorbital buttressing. The last two features suggest clearly that the preferred food was tougher and more resistant than that utilized by other eupelycosaurian taxa of similar skull size.

   With the exception of isodonty, the morphology of the marginal tooth series of *Edaphosaurus* has been ignored completely when the hypothesis of herbivory is considered. Although dental

morphology is the foremost indicator of probable diet in fossil tetrapods, the evidence for edaphosaurid herbivory provided by tooth plate morphology has overshadowed that of the marginal dentition. This is unusual, given that well preserved maxillary teeth from the Briar Creek Bonebed were figured and described briefly by Williston (1916). However, the marginal teeth of *Edaphosaurus* were described by Romer and Price (1940) as slightly bulbous pegs, and hence were considered unremarkable.

The Geraldine material reveals that marginal teeth of *Edaphosaurus* have several features that are consistent with a diet of terrestrial plant foliage. Notably, cutting edges are present on the marginal teeth, and they are inclined obliquely with respect to the long axis of the tooth row. Although this feature is found in some carnivorous reptiles (Molnar and Farlow 1990) as well as in many herbivorous ones, the marginal teeth of *Edaphosaurus* widen slightly before tapering to form distinctive shoulders, a trait that is never observed in the teeth of carnivorous types (Galton 1986). Furthermore, the cutting edges of unworn teeth bear fine, oblique serrations that are emphasized by grooves on the lingual surfaces of the teeth. The oblique orientation of the grooves suggests that the serrations here are strikingly similar to those found in other herbivorous reptiles, which are directed more-or-less apically, rather than those of carnivorous reptiles, which are invariably perpendicular to the cutting edge of the teeth (Galton 1986). Interestingly, many of the mature teeth in *Edaphosaurus* have lost their serrations, which suggests that the preferred food was highly abrasive and possibly siliceous.

The general morphology of the tooth plates is relatively well known (Romer and Price 1940; Modesto and Reisz 1992), and the hypothesis that the plates served to crush food has not been disputed. Romer and Price (1940) observed that the articular facet of the articular was longer antero-posteriorly than that of the quadrate, and suggested that propaliny was probably present. However, they did not elaborate on the subject. The cranial materials described here suggest that propalinal movement of the mandible was a necessary component to the grinding action of the tooth plates. Further evidence for propalinal movement of the jaws comes from additional morphology of the jaw suspension, the orientation of the tooth plates with respect to the jaw suspension, and palatal tooth wear. The strongest evidence for fore-and-aft jaw movement is suggested by the nature of the contact between the quadrate and the articular. The condylar portion of the former is modified from the bicondylar type characteristic of other eupelycosaurs: instead of two parasagittally-aligned, elongate condyles, there is a single, broad, saddle-shaped articulating surface. The trough of the quadrate condyle sat in tongue-and-groove fashion over the antero-posterior ridge that bisects the opposing articulating facet on the articular. As noted by Romer and Price (1940), the articular was clearly capable of antero-posterior translation relative to the quadrate since its articulating facet is approximately 50 per cent. longer antero-posteriorly than that of the quadrate; the overall antero-posterior range of movement appears to have been no more than about 8 mm, or approximately 7 per cent. of the antero-posterior length of the mandible. The long axes of the palatal and mandibular tooth plates are roughly parallel to the plane of articulation between the articular and the quadrate in medial view (Text-figs 2, 17), whereas those of the marginal tooth rows are set at an angle to the axis of translation. This suggests that propaliny was associated with the requirement for an efficient grinding mechanism, and evidence from palatal tooth wear supports this postulate. The tips of most well-preserved tooth plate teeth display oblique bevelling of their lateral and medial surfaces; bevelling of the anterior or posterior surfaces of tooth plate teeth, which would be expected to be equally common if plate occlusion was strictly orthal, is less frequent. An SEM study of tooth plate teeth referable to *E. boanerges* (Olson *et al.* 1991) suggests strongly that the wear was induced by propalinal tooth plate movement. Propalinal jaw action may also have been responsible for the wear seen on the lingual surfaces of the marginal teeth. The bevelling present on the ventral surfaces of the recumbent, posterior maxillary teeth must have resulted from the opposing dentary teeth sliding antero-posteriorly beneath them; it is unlikely that such uniform wear was incurred during orthal occlusion. Since the above-mentioned morphological evidence is identifiable in cranial material of all members of the genus (where preserved), propaliny can be considered an adaptation uniting the species of *Edaphosaurus*.

The jaw musculature must have been arranged appropriately in *Edaphosaurus* in order to effect fore-and-aft movement of the mandibles. The temporal fenestra is antero-posteriorly expanded, suggesting that posterior fibres of the jaw adductor muscles were inclined at roughly 45° relative to the long axis of the mandible, and therefore may have served to draw the mandible posteriorly. The anterior pterygoideus muscle, originating from the dorsal surface of the large palatal tooth plate, probably served to pull the mandible anteriorly. A similar arrangement is hypothesized to power propalinal jaw movement in dicynodonts (Crompton and Hotton 1967; King *et al.* 1989). Interestingly, propalinal jaw movement may have been assisted by a posteriorly-directed muscle attaching to the vertical keel of the angular. The posterior third of the keel is thickened and crenulated, suggesting that it may have served for muscular attachment. The strong evidence for propalinal jaw movement, and its requirement for suitably orientated muscles to power the propalinal jaw stroke, suggests that this may have been the case. Such a peculiar muscular arrangement was suggested also for dinocephalian therapsids, although the hypothetical muscle was considered to assist only in abducting the mandible (Kemp 1982).

Lastly, the peculiar arrangement of the marginal tooth rows, due to the twisting of the alveolar ridges of the maxilla and dentary in all species of *Edaphosaurus*, is an unusual development among Palaeozoic tetrapods; there are no extant analogues that may suggest a reason for such a remarkable condition. What is noteworthy is that the orientation of the marginal teeth alters immediately anterior to the tooth plates, which implies that only the marginal teeth anterior to the tooth plates could function effectively to crop small pieces from food items; the recumbent marginal teeth adjacent to the plates could not take part in cropping actions, as their tips would not be able to slide past their fellows in the opposing dentition. These recumbent maxillary and dentary teeth may have added respectively their lingual and labial surfaces to the total area of the neighbouring tooth plates, as the lingual surfaces of well preserved procumbent marginal teeth display wear suggestive of such contact. However, since the long axes of the marginal tooth rows are positioned at an angle to the axis of propalinal movement, the posterior marginal teeth would only have been able to occlude at the end of the forward translation of the mandible during propalinal jaw movement, as the upper and lower tooth rows would have been drawn apart when the mandible moved posteriorly. Their contribution to the grinding phase of food processing, however, would have been minor compared to that of the tooth plate dentition. Nevertheless, the division in function between the anterior and posterior regions of the marginal tooth rows in this early amniote genus is quite remarkable.

Marginal tooth morphology, tooth plate organization, the evidence for propaliny, and the suite of non-dental features which are shared with known herbivorous reptiles form a character complex that strongly supports the hypothesis of herbivory in *Edaphosaurus*. The feeding system of this genus appears to be the most specialized of the early Permo-Carboniferous synapsids. Food processing appears to have been comprised of two distinct steps: (1) the anterior marginal dentition served to section bite-sized pieces from terrestrial plants; and (2) the tooth plates served to pulverize the food via propalinal jaw action. Grinding presumably prepared the food for fermentative digestion. Among other Palaeozoic tetrapods, compelling evidence for propalinal jaw action has been presented only for dicynodonts, which appear much later in the Upper Permian (King *et al.* 1989). *Edaphosaurus*, therefore, is the oldest amniote known to have been capable of fore-and-aft translation of the mandible. Perhaps more importantly, *Edaphosaurus* is further distinguished as the oldest known amniote to exhibit a dual-purpose, two-step feeding system. Such partitioning of function in the oral region is not seen elsewhere in amniotes until cynodont therapsids appear at the close of the Permian (Kemp 1982).

REFERENCES

BERMAN, D. S 1979. *Edaphosaurus* (Reptilia, Pelycosauria) from the Lower Permian of northeastern United States, with description of a new species. *Annals of the Carnegie Museum*, **48**, 185–202.

—— and REISZ, R. R. 1982. Restudy of *Mycterosaurus longiceps* (Reptilia, Pelycosauria) from the Lower Permian of Texas. *Annals of the Carnegie Museum*, **51**, 423–453.

BRINKMAN, D. B. and EBERTH, D. A. 1983. The interrelationships of pelycosaurs. *Breviora*, **473**, 1–35.

BROOM, R. 1910. A comparison of the Permian reptiles of North America with those of South Africa. *Bulletin of the American Museum of Natural History*, **28**, 197–234.

CARROLL, R. L. 1988. *Vertebrate paleontology and evolution*. W. H. Freeman and Co., New York, 698 pp.

CASE, E. C. 1906. On the skull of *Edaphosaurus pogonias* Cope. *Bulletin of the American Museum of Natural History*, **22**, 19–26.

—— 1907. Revision of the Pelycosauria of North America. *Carnegie Institution of Washington, Publication*, **55**, 1–176.

—— 1918. A mounted skeleton of *Edaphosaurus cruciger* Cope, in the geological collection of the University of Michigan. *Occasional Papers of the Museum of Zoology, University of Michigan*, **62**, 1–8.

COPE, E. D. 1882. Third Contribution to the history of the Vertebrata of the Permian Formation of Texas. *Proceedings of the American Philosophical Society*, **20**, 447–461.

CROMPTON, A. W. and HOTTON III, N. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). *Postilla*, **109**, 1–51.

EBERTH, D. A. 1985. The skull of *Sphenacodon ferocior*, and comparisons with other sphenacodontines (Reptilia, Pelycosauria). *Circular of the New Mexico Bureau of Mines and Mineral Resources*, **190**, 1–39.

GALTON, P. M. 1986. Herbivorous adaptations of Late Triassic and Early Jurassic dinosaurs. 203–221. *In* K. PADIAN (ed.). *The beginning of the age of dinosaurs*. Cambridge University Press, Cambridge, 378 pp.

HENTZ, T. F. 1988. Lithostratigraphy and paleoenvironments of upper Paleozoic red beds, North-Central Texas: Bowie (new) and Wichita (revised) Groups. *University of Texas, Austin, Bureau of Economic Geology Report of Investigations*, **17**, 1–55.

KEMP, T. S. 1982. *Mammal-like reptiles and the origin of mammals*. Academic Press, London, 363 pp.

KING, G. M., OELOFSEN, B. W. and RUBIDGE, B. S. 1989. The evolution of the dicynodont feeding system. *Zoological Journal of the Linnean Society*, **96**, 185–211.

LAURIN, M. 1993. Anatomy and relationships of *Haptodus garnettensis*, a Pennsylvanian synapsid from Kansas. *Journal of Vertebrate Paleontology*, **13**, 200–229.

—— and REISZ, R. R. 1990. *Tetraceratops* is the oldest known therapsid. *Nature*, **345**, 249–250.

MODESTO, S. P. 1992. Did herbivory foster early amniote diversification? *Journal of Vertebrate Paleontology, Abstracts*, **11**, 49A.

—— 1994. The Lower Permian synapsid *Glaucosaurus* from Texas. *Palaeontology*, **37**, 51–60.

—— and REISZ, R. R. 1990. A new skeleton of *Ianthasaurus hardestii*, a primitive edaphosaur (Synapsida: Pelycosauria) from the Upper Pennsylvanian of Kansas. *Canadian Journal of Earth Sciences*, **27**, 834–844.

—— —— 1992. Restudy of Permo-Carboniferous synapsid *Edaphosaurus novomexicanus* Williston and Case, the oldest known herbivorous amniote. *Canadian Journal of Earth Sciences*, **29**, 2653–2662.

MOLNAR, R. E. and FARLOW, J. O. 1990. Carnosaur paleobiology. 210–224. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, 773 pp.

MUNK, M. and SUES, H.-D. 1993. Gut contents of *Parasaurus* (Pareiasauria) and *Protorosaurus* (Archosauro-morpha) from the Kupferschiefer (Upper Permian) of Hessen, Germany. *Paläontologische Zeitschrift*, **67**, 169–176.

OLSON, E. C. 1986. Relationships and ecology of the early therapsids and their predecessors. 47–60. *In* HOTTON III, N., MCLEAN, P. D., ROTH, J. J. and ROTH, E. C. (eds). *The ecology and biology of mammal-like reptiles*. Smithsonian Institution Press, Washington, 326 pp.

—— HOTTON III, N. and BEERBOWER, J. R. 1991. Wear of tetrapod teeth as indication of Lower Permian herbivory. *Journal of Vertebrate Paleontology Abstracts*, **11**, 49A.

OSBORN, H. F. 1903. On the primary division of the Reptilia into two subclasses, Synapsida and Diapsida. *Science*, **17**, 275–276.

REISZ, R. R. 1986. Pelycosauria. *In* WELLNHOFER, F. (ed.). *Handbuch der Paläoherpetologie*, Teil 17A. Gustav Fischer Verlag, Stuttgart, 102 pp.

—— and BERMAN, D. S. 1986. *Ianthasaurus hardestii* n. sp., a primitive edaphosaur (Reptilia, Pelycosauria) from the Upper Pennsylvanian Rock Lake Shale near Garnett, Kansas. *Canadian Journal of Earth Sciences*, **23**, 77–91.

—— —— and SCOTT, D. 1992. The cranial anatomy of *Secodontosaurus*, an unusual mammal-like reptile (Synapsida: Sphenacodontidae) from the early Permian of Texas. *Zoological Journal of the Linnean Society*, **104**, 127–184.

ROMER, A. S. and PRICE, L. I. 1940. Review of the Pelycosauria. Geological Society of America, Special Paper, **28**, 1–538.

ROWE, T. 1988. Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology*, **8**, 241–264.

SANDER, P. M. 1987. Taphonomy of the Lower Permian Geraldine Bonebed in Archer County, Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **61**, 221–236.

WATSON, D. M. S. 1916. Reconstructions of the skulls of three pelycosaurs in the American Museum of Natural History. *Bulletin of the American Museum of Natural History*, **35**, 637–648.

WILLISTON, S. W. 1914. The osteology of some American Permian vertebrates. 1. *Contributions from Walker Museum*, **1**, 107–162.

—— 1916. Synopsis of the American Permo-Carboniferous Tetrapoda. *Contributions from Walker Museum*, **1**, 193–236.

S. P. MODESTO

Department of Zoology, Erindale College
University of Toronto, Mississauga
Ontario, Canada L5L 1C6

ABBREVIATIONS USED IN THE TEXT-FIGURES

ac	anterior coronoid		pf	postfrontal
an	angular		pl	palatine
ana	atlantal neural arch		po	postorbital
ar	articular		pop	paroccipital process
ar/ss	sutural surface for articular		pra	prearticular
bcr	basicranial recess		pra/ss	sutural surface for prearticular
bo	basioccipital		prf	prefrontal
bpt	basipterygoid process		prm	premaxilla
bps	basiparasphenoid		pro	proötic
cu	cultriform process		pt	pterygoid
d	dentary		q	quadrate
ds	dorsum sella		qfl	quadrate flange of pterygoid
ec	ectopterygoid		qj	quadratojugal
eo	exoccipital		s	stapes
ep	epipterygoid		sa	surangular
f	frontal		sa/ss	sutural surface for surangular
fo	fenestra ovalis		sm	septomaxilla
icf	internal carotid foramen		so	supraoccipital
j	jugal		sp	splenial
l	lacrimal		sq	squamosal
lpso	lateral process of supraoccipital		st	supratemporal
m	maxilla		t	tabular
mj	medial process of jugal		t/ss	sutural surface for tabular
n	nasal		v	vomer
op	opisthotic		vp prf	ventral process of prefrontal
p	parietal		vf op	ventral flange of opisthotic
pc	posterior coronoid			

APPENDIX 1

Description of characters used in the analysis. Characters are listed in order of their location on the skull, the mandible, and the postcranial skeleton.

1. Marginal teeth: taper gradually (0) or are slightly bulbous (1). The marginal teeth of all *Edaphosaurus* species are slightly swollen distally. The teeth of the outgroup taxa taper gradually to their distal tips, and represent the plesiomorphic condition.
2. Marginal teeth: cutting edges are absent (0) or present (1) on mesial and distal surfaces. The marginal teeth of the Texan species of *Edaphosaurus* feature cutting edges on their mesial and distal surfaces. This character is indeterminable in *E. novomexicanus*. No cutting edges are present on the teeth of the outgroup taxa.
3. Premaxillary dentition: larger than (0) or equal to or smaller than (1) the maxillary teeth in basal cross-section. On the basis of basal cross-sectional diameter, the premaxillary teeth are roughly equal to the maxillary teeth in size in both *Glaucosaurus* and *Edaphosaurus*. Because premaxillary teeth are unknown in *Ianthasaurus*, this character may diagnose Edaphosauridae. The presence of premaxillary teeth larger than maxillary teeth (except caniniforms) is primitive for eupelycosaurs.
4. Caniniform region: present (0) or absent (1). Neither *Glaucosaurus* nor *Edaphosaurus* possesses a caniniform region. Accordingly, the presence of a caniniform region is the primitive condition.
5. Caniniform tooth: absent (0) or present (1). There is no caniniform tooth in either *Glaucosaurus* or *Edaphosaurus*. The presence of a caniniform represents the primitive condition for edaphosaurids.
6. Maxilla: long, extends past orbit (0) or short, does not extend beyond posterior orbital margin (1). The derived condition diagnoses here the clade of Edaphosauridae plus Sphenacodontia. The long maxilla of *Glaucosaurus* is a reversal (Modesto 1994).
7. Maxillary and dentary alveolar ridges: straight (0) or twisted (1). The alveolar ridges of the maxillae and dentaries of all members of *Edaphosaurus* are twisted such that the orientation of the marginal dentition becomes laterally directed as one progresses posteriorly. The marginal teeth of the outgroup taxa are vertically directed, representing the primitive condition.
8. Prefrontal: ventral process tongue-like (0) or expanded medially (1). In *Glaucosaurus* and *Edaphosaurus* the ventral process of the prefrontal is greatly expanded medially, forming most of the antorbital buttress that characterizes both taxa. The presence of a prefrontal ventral process that is transversely slender is plesiomorphic.
9. Frontal: lateral lappet broad, antero-posterior width no less than one-quarter frontal sagittal length (0) or narrow, antero-posterior width no less than one-ninth frontal sagittal length (1). The lateral lappet of the frontal is remarkably slender in the Texan edaphosaurids, displaying an antero-posterior width approximately one-ninth the sagittal length of the frontal. The lateral lappet of *Haptodus* has an antero-posterior width roughly one-fifth the length of the frontal, whereas the same figure for the edaphosaurids *Edaphosaurus novomexicanus* and *Ianthasaurus* is approximately one-quarter. Although varanopseids are not considered to possess a lateral lappet (Brinkman and Eberth 1983), the frontal of *Mycterosaurus* has a broad contribution to the orbital rim. This character cannot be determined in *Glaucosaurus*.
10. Supraorbital margin: weakly developed, interorbital width less than frontal sagittal length (0) or expanded laterally, interorbital width 50 per cent. greater than frontal sagittal length (1). The supraorbital margin of *Edaphosaurus* is a broad shelf formed by the prefrontal, frontal, and postfrontal. The transverse breadth of the supraorbital margin is roughly 75 per cent. of the antero-posterior length of the frontal, and, accordingly, the orbits are concealed in dorsal view. The supraorbital margins are weakly developed or absent in the other genera, their transverse breadth lying between 26 per cent. and 46 per cent. of the sagittal length of the frontal, and the orbits are clearly visible in dorsal view.
11. Parietal: lateral margin roughly straight or convex (0) or deeply concave (1) in dorsal aspect. The lateral edge of the parietal is deeply embayed in dorsal aspect in all species of *Edaphosaurus*. In *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* the lateral margin of the parietal is straight to markedly convex, interpreted here as a plesiomorphy.
12. Postorbital: contacts (0) or separate from (1) squamosal. The postorbital posterodorsal process in *E. boanerges*, *E. cruciger* and *E. pogonias* is short and does not contact the squamosal. Since the state of this character cannot be determined in either *E. novomexicanus* or *Glaucosaurus*, it may diagnose a more inclusive node with Edaphosauridae. The outgroup taxa are plesiomorphic in that the postorbital contacts the squamosal.

13. Quadratojugal: large and forms ventral margin of posterior cheek (0) or small and covered laterally by squamosal (1). The derived state diagnoses the clade of Edaphosauridae plus Sphenacodontia (*sensu* Reisz *et al.* 1992). This character cannot be determined in *Glaucosaurus*.

14. Quadrate: condyles distinct, separate (0) or confluent, forming a saddle-shaped articulating facet (1). The articulating surface of the quadrate is a single, broad articulating surface that is yoke-shaped in posterior aspect in all *Edaphosaurus* species. Two elongate, rounded ridges present as condyles represents the primitive condition.

15. Jaw suspension: at level of (0) or offset ventrally from (1) maxillary tooth row. In all species of *Edaphosaurus* the jaw suspension is positioned far below the level of the upper tooth row. This is easily demonstrated as a ratio between the distance the jaw suspension lies ventral to the longitudinal axis of the upper marginal tooth row and the length of the cheek (taken along the longitudinal axis of the upper tooth row). In *Edaphosaurus* this figure is approximately 29 per cent. The jaw suspensions of the other genera are primitive in that they lie slightly below the longitudinal axes of their respective upper tooth rows, with a jaw suspension depth falling between 3 per cent. and 12 per cent. of the length of the cheek.

16. Skull: long, eight dorsal centra or more in length (0), or short, five dorsal centra or less in length (1). The skulls of all *Edaphosaurus* species are relatively short, being less than five dorsal centra in length. The skulls of *Ianthasaurus* and the outgroup taxa are at least eight dorsal centra in length; relatively long skulls are therefore primitive.

17. Postorbital region: shorter than (0) or equal to or longer than (1) antorbital region. In all species of *Edaphosaurus*, the antero-posterior length of the postorbital region of the skull is equal to, or even marginally greater than, the antorbital length. The postorbital regions of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are less than half the length of their respective antorbital regions. A postorbital region that is shorter than antorbital length is a plesiomorphy of eupelycosaurs.

18. Pterygoid: transverse flange present (0) or absent (1). A transverse flange is absent from the pterygoid in *Glaucosaurus* and *Edaphosaurus*. Because the palate is unknown for *Ianthasaurus*, this character may diagnose Edaphosauridae. The presence of a transverse pterygoid flange is plesiomorphic for eupelycosaurs.

19. Tooth plates: absent (0) or present (1). *Edaphosaurus novomexicanus* possesses palatal tooth plates that undoubtedly contacted similar plates on the mandibles. Palatal and mandibular tooth plates are present in *E. boanerges*, *E. cruciger*, and *E. pogonias*. The palatal plate is formed by the palatine, ectopterygoid and the pterygoid, whereas the mandibular tooth plate is formed by the anterior and posterior coronoids, and the prearticular. Tooth plates are not present in the outgroup taxa; the absence of tooth plates is the primitive condition for eupelycosaurs.

20. Mandible: dorso-ventral height one-quarter or less (0) or one-third or greater (1) total length. The mandibles of the three Texan edaphosaurs are relatively deep, with a height no less than one-third the total length of the mandible. In contrast, those of *Ianthasaurus*, *Mycterosaurus* and *Haptodus* are relatively slender, with a height equal to or less than one-quarter the total length of the mandible. Since the posterior ends of both the skull and the mandible are absent in *Glaucosaurus*, the character state cannot be determined for this taxon. The mandible is unknown in *E. novomexicanus*.

21. Dentary: comprises 70 per cent. or more (0) or 66 per cent. or less (1) of the mandibular antero-posterior length. The dentaries of *Edaphosaurus cruciger* and *E. pogonias* are 66 per cent. and 63 per cent. of the total length of the mandible, respectively. The dentary of *E. boanerges* is about 70 per cent. of the length of the mandible, and this figure in *Haptodus* and *Mycterosaurus* is roughly 80 per cent. The mandibles of *Ianthasaurus* and *Glaucosaurus* are inadequately known, but resemble more closely those of carnivorous eupelycosaurs. The presence of a dentary that is more than two-thirds the length of the mandible represents the primitive condition for *Edaphosaurus*.

22. Splenial: lateral exposure one-fifth or less (0) or one-third or more (1) the height of the anterior end of the mandible. The splenial is deep and occupies the lower one-third of the anterior end of the mandible in lateral view in those species of *Edaphosaurus* for which mandibular material is available. In contrast, the splenial has only a slender, antero-posteriorly elongate lateral exposure in the outgroup taxa.

23. Cervical centra: equal to or longer than (0) or shorter than (1) mid-dorsal centra. The cervical centra are notably shorter than those of the dorsal centra in *Edaphosaurus*. In contrast, the cervical vertebrae are slightly longer antero-posteriorly than the dorsal vertebrae in *Ianthasaurus* (Reisz and Berman 1986). The cervicals and dorsal are approximately equal in length in *Haptodus* and *Mycterosaurus*. The character state for this and the following characters cannot be determined in *Glaucosaurus*.

24. Presacral neural spines: short (0), or long, more than five times the height of the centrum (1). The presacral neural spines are greatly elongated in all edaphosaurid taxa for which postcrania is available. In the

outgroup taxa, neural spines are always less than five times the height of the centrum. Other Permo-Carboniferous synapsids feature greatly elongate neural spines, but these have evolved independently (Reisz *et al.* 1992).

25. Presacral neural spines: laterally compressed (0) or subcircular (1) in distal cross section. Except for a short basal portion which is expanded slightly antero-posteriorly, the presacral neural spines of *Ianthasaurus* and *Edaphosaurus* are subcircular in distal cross-section. The presence of blade-like neural spines is primitive for eupelycosaurian synapsids.

26. Presacral neural spines: lateral tubercles absent (0), present and moderately developed (1), present and gall-like (2). The elongate neural spines of the presacral vertebrae of *Ianthasaurus* and *Edaphosaurus* feature laterally-directed processes. Swollen, gall-like tips are present on many of the tubercles of both *E. cruciger* and *E. pogonias*. The lateral surfaces of the presacral neural spines of the outgroup taxa are devoid of processes, and represent the plesiomorphic condition.

27. Presacral neural spines: anterior spines are slender (0) or club-shaped (1). The distal ends of the neural spines of the anterior presacral vertebrae of *E. cruciger* and *E. pogonias* are slightly thickened laterally and expanded antero-posteriorly to twice the basal diameter of the subcircular portion of the spine. The expansion is so great that the spines resemble pegged clubs. Romer and Price (1940) report a definite, albeit slight, sagittal expansion of the cervical spines of *E. boanerges*, but clearly not to the extent seen in the other Texan species.

28. Neural arches: excavated (0) or not excavated (1). The neural arches of all *Edaphosaurus* species do not display the shallow excavations present in those of *Ianthasaurus*, *Haptodus*, or *Mycterosaurus*. The presence of excavations on neural arches is plesiomorphic for eupelycosaurs.

29. Dorsal vertebrae: transverse processes moderately developed (0) or elongate (1). The transverse processes of the presacral vertebrae of *Edaphosaurus* are elongate. The transverse processes of the outgroup taxa are relatively short transversely, and represent the primitive condition for eupelycosaurs.

30. Sacral and caudal vertebrae: neural spine tips smoothly finished (0) or rugose (1). The distal tips of the sacral and caudal neural spines in *Edaphosaurus* are roughened with crenulated edges. The tips of the sacral and caudal neural spines in *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are plesiomorphic in that they are smoothly finished.

31. Sacral and caudal vertebrae: neural spines smooth-sided (0) or with longitudinal ridges (1). The lateral surfaces of the sacral and caudal neural spines of *Edaphosaurus* feature rough, longitudinal ridges. The lateral surfaces of the caudal neural spines of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are plesiomorphic in that they are smoothly finished.

32. Caudal vertebrae: neural spines are rectangular in lateral aspect (0) or expanded sagittally (1). The distal ends of the caudal neural spines of *Edaphosaurus* are expanded antero-posteriorly. The caudal neural spine tips of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are plesiomorphic in that they are squared in lateral aspect.

33. Caudal vertebrae: neural spines are short and squared (0) or tall and pointed (1) in lateral aspect. The distal tips of the caudal neural spines of all *Edaphosaurus* species are tall (at least twice the height of the neural arch proper) and taper to pointed tips. The neural spines of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are plesiomorphic in that distally they are squared in lateral aspect, and are never taller than their respective pedicels.

34. Dorsal ribs: curved proximally only (0) or curved throughout length (1). The dorsal ribs of all species of *Edaphosaurus* are strongly curved throughout their length. Only the proximal regions of the dorsal ribs of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are strongly curved; the distal parts of the ribs are only slightly bowed.

35. Dorsal ribs: tubercula well developed, flange-like (0) or reduced to low tuberosities (1). The tubercular heads of the dorsal ribs of all species of *Edaphosaurus* are present only as small rugosities. The tubercular heads of the dorsal ribs of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are normally developed as prominent projections of bone, representing the primitive condition for eupelycosaurs.

36. Ilium: anterodorsal process smaller than posterodorsal process and convex in lateral view (0) or equal to posterodorsal process in size and triangular in lateral view (1). The ilia of the Texan edaphosaurids have triangular, spade-like anterodorsal processes that equal the posterodorsal processes in size. The iliac anterodorsal processes of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are low and convex in lateral aspect, and never approach the size of the posterodorsal processes.

APPENDIX 2

Distribution of the character states among the eight taxa examined in the analysis. The numbers in the top column (1–36) refer to the characters described in Appendix 1. A question mark indicates that the character state could not be determined because of missing data.

Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Taxon																		
Mycterosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haptodus	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Ianthasaurus	0	0	?	0	0	1	0	0	0	0	0	0	1	?	0	0	0	?
Glaucosaurus	0	0	1	1	1	0	0	1	?	0	?	?	?	?	?	?	?	1
E. novomexicanus	1	?	?	1	1	1	1	1	0	1	1	?	1	1	1	1	1	1
E. boanerges	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
E. cruciger	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
E. pogonias	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Character FS48 number	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Taxon																		
Mycterosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haptodus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ianthasaurus	0	0	0	?	0	1	1	1	0	0	0	0	0	0	0	0	0	1
Glaucosaurus	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
E. novomexicanus	1	?	?	?	1	1	1	1	0	1	1	1	1	1	1	1	1	?
E. boanerges	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
E. cruciger	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1
E. pogonias	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1